THE PHYLOGENY OF THE SCOMBROID FISHES

Volume 1: Text

Kenneth Anthony Monsch

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ABSTRACT

The borders of, and the relationships within the teleost suborder Scombroidei are disputed. There are three competing relationships that strongly conflict at some points. An attempt has been made to solve the conflict by conducting a new morphological analysis, introducing for the first time data of fossil taxa. A systematic palaeontology of scombroids is presented, including several revisions. I also present a preliminary phylogeny that provides interesting results, but needs reworking to confirm the relationships presented. Preliminary results are that *Sphyraena* is not a scombroid, billfishes are advanced scombrids closely related to *Acanthocybium*, Trichiurinae and Gempylinae together form a monophyletic clade of trichiurids, and Thunnini are advanced Sardinae. The results of incorporating fossils in the cladistic analysis are mixed. Most fossils have a negative impact on the resolution of the cladogram, but the fossil *Eothynnus* strengthens the hypothesis that billfishes are closely related to *Acanthocybium*. The endothermic *Gasterochisma* was not included in the final analysis. Endothermy evolved twice independently in billfishes and tunas. The preliminary cladogram presented shows relationships that are a mix of those expressed in other previously published phylogenies, and some that are for the first time expressed as presented here. When a robust phylogeny of Recent and fossil scombroids is produced, it can be used as a tool to assess biodiversity. To overcome the problem of missing data, techniques such as safe taxonomic deletion (STD) and reduced cladistic consensus (RCC) have been employed. STD successfully deleted some fossil taxa safely, but I argue that the methodology could be improved. A well-resolved RCC tree is not obtained, but I do not doubt the efficiency of the technique. The fact that my data set needs reworking is thought to be the reason most consensus techniques, including RCC provide poorly resolved cladograms.

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Many people have contributed to the completion of this thesis, without their input it might not have materialised. I express here my gratitude to these persons.

Before I thank those who are physically visible, I feel I should thank someone who is not. Lord God for, thank You for leading me here and giving me a chance to investigate the nature You made. Faith in You and belief in evolution are not mutually exclusive to me. Many conflicts would be resolved if more people accept this.

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Last, and never least, I thank my parents for their moral and certainly their financial support and my brother Ruben for his constant interest in my well-being.

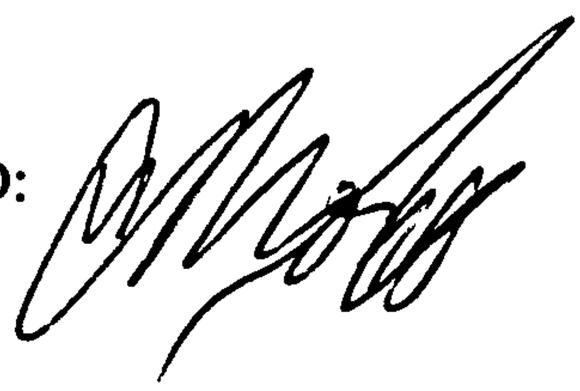
Have I still forgotten someone? That's not my fault then. You should've shouted louder.

AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the Regulations of the University of Bristol. The work is original except where indicated by special reference in the text and no part of the dissertation has been submitted for any other degree.

Any views expressed in the dissertation are those of the author and in no way represent those of the University of Bristol.

The dissertation has not been presented to any other University for examination either in the United Kingdom or overseas.

SIGNED: 

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INTRODUCTION

The scombroids (suborder Scombroidei, order Perciformes) include economically important fishes such as tunas (Thunnini), bonitos (Sardini), mackerels (Scombrini) and billfishes (Istiophoridae and Xiphiidae), as well as other well known fishes such as Trichiuridae and Gempylidae. The taxa involved in this study are discussed and listed in Chapter 1. The interrelationships of the members of this group are not at all clear. Different hypotheses have been proposed on scombroid relationships, which show significant differences in the boundaries of the group to be recognised as scombroids and in the relationships within that group. The different opinions will be outlined at the start of Chapter 2.

The scombroids contain, amongst others, some of the very few known endothermic fishes, namely the tunas (except maybe *Allothunnus* Serventy, 1948; see § 4.1), *Gasterochisma melampus* Richardson, 1845, and the billfishes. The evolution of endothermy in the scombroids is not well understood. The phenomenon appears in three lineages that are believed to have evolved separately, with three different strategies for maintaining a high temperature in either the whole body or the cranial region alone. A review of previous studies concerning aspects of endothermy in these fishes can be found in Chapter 4. A major question is: how many times has scombroid endothermy evolved? Has it evolved three times, independently, or just once and then modified or reversed to ectothermy in some lineages? Understanding of this extraordinary phenomenon and the pattern of its evolution should contribute to a good understanding of this group.

The research presented in this thesis is an attempt to solve the systematic problems of the scombroids. I believe that incorporating the fossils in the study, which has not been done before for this group, can shed new light on the systematic divisions of scombroids. Bannikov (1985) compared fossil scombrids of the former USSR to fossil taxa from other regions and Recent taxa, to draw conclusions on phylogenetic relationships. However, his conclusions are based on comparisons, within a framework of what appears to be an overall-similarity approach, in which many assumptions are made. Moreover, his data of taxa other than former USSR scombrids are all drawn from the literature. Nowhere in the materials section of his monograph are specimens of Recent taxa mentioned, nor fossil taxa of scombroids from other areas than the former Sowjet Union. I believe that phylogenetic relationships can be better assessed by means of reconstructing cladograms, in which clades are determined by synapomorphies, which are found or confirmed after the analysis is finished. Also, I believe that statements on phylogenetic relationships are better supported if a large number of specimens is used to supply data. Considerations on combining Recent and fossil evidence are given in Chapter 3. This is the aim of the studies on which this thesis is based: an

attempt to solve questions on the systematic relationships and character evolution of scombroids, by means of incorporating evidence not used before. Scombroid fishes lend themselves perfectly for an investigation of this sort. On one hand there is a thorough knowledge of Recent scombroids in terms of their anatomy and osteology. On the other hand, scombroids have a good fossil record. Scombroid fossils are known from the late Palaeocene/early Eocene to the Pleistocene and are well known from North America, Europe, Africa, Asia and Australasia. Within this wide cosmopolitan range, scombroid fossils are the best known from England, Belgium, Switzerland and the former USSR.

Knowledge of the interrelationships of these economically important fishes is beneficial, because cladograms and biogeography can be tools to determine appropriate conservation strategies for the different taxa in their habitats (Humphries *et al.*, 1995). Knowledge of the evolution of the extraordinary metabolic strategies of some scombroids (endothermy) will hopefully be achieved, and is intended to contribute to a better understanding of the evolution of aspects of the physiology of these animals.

As said above, and discussed in detail in Chapter 2, above, there is no uniformity of opinion about scombroid relationships. It is hoped that incorporating the fossils in the study can shed new light on the systematic divisions of scombroids. In these studies, recently published phylogenetic methodologies such as those of Wilkinson, 1995; Wilkinson & Benton, 1995 and 1996, will be used. These methods help to resolve the problem of missing data, which occurs frequently when dealing with fossils. The algorithms in question help to decide with problematic characters or taxa can be safely deleted from the cladistic analysis and a relatively new method to compute consensus trees (see also Chapter 8).

The intention of the research presented in this thesis can be summed up as follows. Phylogenetic hypotheses of scombroids based on Recent material have so far been unable to provide a consensus of opinion on scombroid relationships. The competing hypotheses differ significantly. In an attempt to solve this problem, previously ignored data, based on fossil material, is incorporated in a new cladistic analysis. It is hoped that this will bring clarity into the controversies, and provide a new look at interesting evolutionary puzzles such as the evolutionary pattern of endothermy.

CHAPTER 1: SCOPE OF THE STUDIED TAXA

1.1 Focus

The taxic level chosen to be examined is the genus. Generally, the assignment of species to their genera does not seem to be in question. However, it is not always clear whether some genera belong to a certain tribe or another. An example is *Lepidocybium* Gill, 1862, which Johnson (1986) excluded from the gempylids, in which they are normally included, to create a monotypic tribe Lepidocybiini. Concerning this point, the tunas deserve some closer attention. It is generally accepted nowadays that the tuna genus *Thunnus* South, 1845, as originally diagnosed, is not to be split up into several genera. This trend of splitting had been started by Kishinouye (1923). Still, Kishinouye's idea that the original *Thunnus* can be split up has not gone. There is still some confusion regarding the systematic divisions of the tunas up to this day (see §1.3). Unfortunately, the time limit of this study has not allowed me to study the tunas at the species level, which I intended to do first. It is hoped that a future study will allow this to be done. For the purpose of this thesis I will here consider *Thunnnus* as a recognised monophyletic genus.

1.2 List of taxa

Below follows a list of the taxa involved in this study. Table 1.1 contains the outgroup taxa (reasons for choosing these taxa as outgroup are given in §1.5), Table 1.2 trichiurids, Table 1.3 gempylids, Table 1.4 billfishes and Table 1.5 scombrids. In Table 1.6 are included fossil taxa whose phylogenetic position cannot be determined readily based on comparison with Recent taxa. The position

Table 1.1. List of outgroup taxa used in this study

Family	Genus, author, year
Coryphaenidae (dolphin fish)	*Coryphaena* Linnaeus, 1758
Carangidae	*Trachurus* Rafinesque-Schmaltz 1810
Luvaridae (louvars)	*Luvarus* Rafinesque-Schmaltz 1810
Scombrolabracidae	*Scombrolabrax* Roule, 1922
Mugilidae (mullets)	*Liza* Jordan & Swain, 1884
	Mugil Linnaeus, 1758
	Valamugil Smith, 1948
Incertae sedis:	
Sphyraenidae (barracudas)	*Sphyraena* Röse, 1793

Table 1.2. List of Trichiuridae (cutlassfishes).

Genus, author, year
†*Anenchelum* De Blainville, 1818
Aphanopus Lowe, 1839
Assurger Whitley, 1933
Benthodesmus Goode & Bean, 1882
Eupleurogrammus Gill, 1862
†*Eutrichiurides* Casier, 1944
Evoxymetopon Gill, 1863
Lepidopus Goüan, 1770
Lepturacanthus Fowler, 1905
Tentoriceps Whitley, 1948
Trichiurus Linnaeus, 1758

Table 1.3. List of Gempylidae (snake mackerels, gemfishes)

Genus, author, year
†*Abadzekhia* Bannikov, 1985
Dicrotus Günther, 1860[1]
Diplospinus Maul, 1948
Epinnula Poey, 1854
Gempylus Cuvier, 1829
Lepidocybium Smith, 1849
Nealotus Johnson, 1865
Neoepinnula Matsubara & Iwai, 1952
Nesiarchus Johnson, 1862
Paradiplospinus Andriashev, 1960
†*Progempylus* Casier, 1966
Rexea Waite, 1911
Rexichthys Parin & Astakhov, 1987
Ruvettus Cocco, 1829
Thyrsites Lesson, 1831[2]
Thyrsitoides Fowler, 1929
Thyrsitops Gill, 1862
Tongaichthys Nakamura & Fuji, 1983

included in an *incertae sedis* section in Table 1.1. Intended as a summary and overview, these tables contain genera, all potential OTUS in the cladistic analysis.

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[1]Commonly known as *Promethichthys* Gill, 1893

[2] Also cited as *Thyrsites* Cuvier, 1832, although this is certainly predated by Lesson's description.

Table 1.4. List of billfishes

Family	Genus, author, year
†Blochiidae	†*Blochius* Volta, 1796
Istiophoridae	*Istiophorus* Lacépède, 1801
	Makaira Lacépède, 1802
	Tetrapturus Rafinesque-Schmaltz, 1810
†Palaeorhynchidae	†*Palaeorhynchus* De Blainville, 1818
	†*Pseudotetrapturus* Danil'chenko, 1960
	†*Homorhynchus* Van Beneden, 1873
†Xiphiorhynchidae	†*Xiphiorhynchus* Van Beneden, 1871
Xiphiidae (swordfish)	*Xiphias* Linnaeus, 1758

Table 1.5 List of scombridae (mackerels)

Tribe	Genus, author, date
Gasterochismatini	*Gasterochisma* Richardson, 1845
Scombrini	†*Scombrinus* Woodward, 1901
	Scomber Linnaeus, 1758
(mackerels)	*Rastrelliger* Jordan & Starks, 1908
Scomberomorini	*Acanthocybium* (Cuvier, 1832)
(Spanish mackerels)	*Grammatorcynus* Gill, 1862
	Scomberomorus Lacépède, 1801
Sardini (bonitos)	*Cybiosarda* Whitley, 1935
	Gymnosarda Gill, 1862
	Sarda Cuvier, 1829
	†*Stereodus* Owen, 1865
	Orcynopsis Gill, 1862
Thunnini (tunas)	*Allothunnus* Serventy, 1948
	Auxis Cuvier, 1829
	Euthynnus Lütken, 1883
	Katsuwonus Kishinouye, 1923
	†"Thunnidae indet." Bannikov, 1985
	Thunnus South, 1845
incertae sedis	†*Eocoelopoma* Woodward, 1901
	†*Eothynnus* Woodward, 1901
	†*Palaeothunnus* Bannikov, 1978
	†*Scombramphodon* Woodward, 1901
	†*Sphyraenodus* Agassiz, 1844
	†*Wetherellus* Casier, 1966
	†*Woodwardella* Casier, 1966

Table 1.6. Fossil taxa whose phylogenetic affinity was unclear before investigation

Family	Genus, author, year
†Euzaphlegidae	†*Palimphyes* Agassiz, 1844
	†*Thyrsion* Jordan, 1920
incertae sedis	†*Acestrus* Woodward, 1901
	†*Aglyptorhynchus* Casier, 1966
	†*Ardiodus* White, 1931
	†*Cylindracanthus* Leidy, 1856
	†*Enniskellinus* Casier, 1966
	†*Hemirhabdorhynchus* Casier, 1949

overview, these tables contain genera, all potential OTUS in the cladistic analysis. For more detail, on species level, I refer to the specimen list (Appendix 1). New fossil taxa, described in this thesis are not included in these tables. They are described in § 7.3 and their phylogenetic position discussed in Chapter 8.

1.3 Non-tuna controversial taxa

In the previous edition of "Fishes of the World" Nelson (1984) mentions the Luvaridae as scombroids, as belonging with the billfishes. However, *Luvarus* shares only one of the six synapomorphies which define the scombroids according to Johnson (1986): the non-protrusible premaxilla. The high degree of fusion in the hypural elements of the tail (as in scombrids) and hypurostegy (the condition where the caudal lepidotrichia almost completely embrace the caudal skeleton, see also § 5.2.4.9) seemed to have been the most important arguments for Regan (1902) to include louvars with scombroids. His other arguments, for example the shape of the ribs, seem ambiguous and unconvincing. Louvars possess, however, 15 of the 19 diagnostic synapomorphies of the acanthuroids. The four remaining synapomorphies that louvars do not to share with acanthuroids are interpreted as reversals (Tyler *et al.*, 1989). Louvars are thus recognised as acanthuroids (Tyler *et al.*, 1986 and 1989). In his later edition of "Fishes of the World", Nelson (1994) agreed with this systematic placement. The scombrid-like tail region of louvars is thought to be the result of parallel evolution. Regan (1909) emphasised hypurostegy as an important synapomorphy of scombrids and louvars, but this phenomenon occurs in a number of diverse, unrelated groups. Hypurostegy is found in amongst others: the holostean Pachycormidae, the Cretaceous Tselfatiidae, the lampridiform Veliferidae and Lampiridae, Carangidae and Scombridae (Le Danois & Le Doanois, 1964 and Patterson, 1968). It is thus concluded that

Luvaridae are not to be included within the scombroids, but are retained as an outgroup of the Scombroidei.

Scombrolabrax. Nelson (1984) included *Scombrolabrax* with the scombroids in his review of the fishes of the world. Parin & Bekker, 1972 included *Scombrolabrax* in a monotypic family Scombrolabracidae, within the superfamily Trichiuroidae, which also includes the Gempylidae and Trichiuridae. In a review of gempylids (Russo, 1983), *Scombrolabrax* is mentioned as a primitive gempylid. Collette *et al.* (1984) state a very close relationship between *Scombrolabrax* and scombroids and include *Scombrolabrax* as their only outgroup taxon. However, *Scombrolabrax* is to be placed in a separate suborder Scombrolabracoidei. Because of mixed percoid and scombroid characters and peculiar autapomorphies in the vertebral skeleton, it does not fit in any other subdivision. It was first noted by Bond & Uyeno, 1981, figs. 1, 2) that *Scombrolabrax*' vertebrae 5-12 are expanded laterally and dorsally to form peculiar bullae which have a close connection to the swimbladder of the fish. This feature is unique and has never before been encountered. The clearest indication that *Scombrolabrax* is not a scombroid is its protractile premaxilla. One of the most striking scombroid synapomorphies is their non-protractile premaxilla (for a description of that condition, see § 5.2.1.2).

Johnson (1986) was the first to include barracudas (Sphyraenidae) with the scombroids. They are mostly considered to be perciform fish closely related to another perciform suborder, the Mugiloidei (De Sylva, 1984). However, they possess all synapomorphies Johnson assigned to the scombroids, even the non-protractile premaxilla. Nelson (1994) supports this inclusion, but many others, such as Finnerty & Block (1994, 1995) do not. In the papers just cited, *Sphyraena* appears as a scombroid outgroup. I accept Johnson's inclusion as a starting point but will analyse the possibility of them being an outgroup to scombroids.

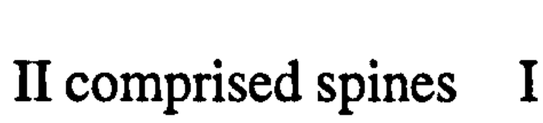
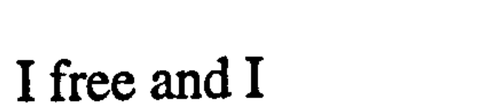
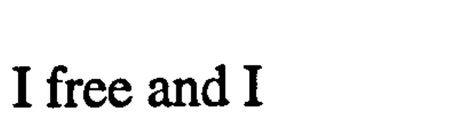
Most workers, such as Collette *et al.* (1984); Johnson (1986), Schultz (1987), Patterson (1993) and Nelson (1994) include billfishes with scombroids but not everyone is convinced that this is corrrect. Nakamura (1985) placed all Recent billfishes in the perciform suborder Xiphioidei. The phylogenetic affinities of the suborder are unknown, but it is not thought to be related to scombrids, gempylids and trichiurids (Nakamura, 1986). Finnerty and Block (1995) produce molecular evidence that excludes billfishes from scombroids. As a starting point, I include billfishes with the ingroup of the cladistic analysis, although the possibility of their being an outgroup or sister group to the scombroids will also be surveyed.

Dicrotus, *Rexea* and *Rexichthys* are highly similar gempylid genera. *Dicrotus* contains one Recent species *Dicrotus prometheus* (Cuvier, 1832) **comb. nov.** (=*Promethichthys prometheus*, see § 7.3 for reasons for nomenclatural change) and one fossil species (see § 7.3). *Rexea* contains six species. *Rexichthys* is also monotypic: *Rexichthys johnpaxtoni* Parin & Astakhov, 1987. The differences among *Dicrotus*, *Rexea* and *Rexichthys* are slight and subtle (Parin, 1989 and 1990; Nakamura & Parin, 1993). Parin (1990) raises the difficulty of identifying the three different genera and discusses whether the differences among the genera are substantial enough to grant a differentiation at genus level. There are many characters that the genera share: vomerine teeth appear in early larval stages, plate-like gill rakers on first arch with 1-3 cusps and one long triple-rooted spinescent angluar raker (see Chapter 5), a vertebral count of 34-36, a pectoral fin ray count of about 13, strongly reduced pelvic fins, XVIII spines in the first dorsal fin, about 17 rays in the second dorsal, 2 anal fin spines followed by 11-17 anal fin rays and a reduced number of finlets (2-3). Differences are noted in Table 1.7. Are the differences noted in Table 1.7 adequate for a differentiation on genus level, are they merely indications of interspecific variation, or do they rather represent differentiation at subgenus level? The lateral lines of *Dicrotus* and *Rexea* for example, seem to show what could be interspecific variation: no dorsal branch, a short dorsal branch and a long dorsal branch.

I am of the opinion that if these genera were lumped into one group, that *Rexichthys* has to be removed from it. *Rexichthys* differs more from *Rexea* and *Dicrotus* than the latter two from each other. The lateral line system of *Rexichthys* is morphologically different in that the ventral branch is located more ventrad and that it possesses the antero-ventral ramus. The ascending part of the ventral branch also ascends more steeply than in *Rexea* and *Dicrotus*.

Superficially, most of the characters that define *Rexea* and *Dicrotus* could be explained by interspecific variation. The case of the lateral line was mentioned before. There is variation between complete and incomplete scale covering and the varying degree up to which the pelvic fin is conserved in adults. There seems to be one character, however, in which there seem to be just two clearly definable states: two comprised anal fin spines (i.e. both spines covered by the fin membrane) in *Dicrotus* and one comprised and one free spine in *Rexea*. In other words, there is one anterior spine, apparently separated from the other fin elements. These comprised fin elements, including an anterior spine, are all covered by the fin membrane. Although differences remain visible among *Dicrotus* and *Rexea*, these differences do not seem substantial enough to erect two seperate genera. However, Parin (1989) ignored a substantial osteological difference among *Rexea* and *Dicrotus* which clearly separates them. *Rexea* possesses a hypural complex with hypural elements 1 and 2 fused, while in *Dicrotus* these are separate. Therefore, in

Table 1.7. Differences among *Dicrotus*, *Rexea* and *Rexichthys*.

	Dicrotus	*Rexea*	*Rexichthys*
lateral line			
scale covering	complete	complete or incomplete	none
vomer teeth	disappear in adults	disappear in adults	stay in adults
pelvic fin	disappears in adults, sometimes pelvic spines as remnant	disappears in adults, sometimes reduced fin remains	disappears completely in adults
anal fin spines	II comprised spines	I free and I comprised spine	I free and I comprised spine
finlets	2	2	3

spite of their strong resemblance, *Dicrotus* and *Rexea* are to be treated as separate genera and their superficial differences (scale covering, lateral line shape) can indeed be used as field characters to separate them.

Gasterochisma. This monotypic genus is generally included in the scombroids, based on such characters as the lepidotrichia of the tail fin covering most of their bony support, and a non-protrusible upper jaw. In the first description of this taxon, it was already considered a scombroid. For a long time, the inclusion of *Gasterochisma* with the scombroids was favoured (see Collette & Nauen, 1983; Collette *et al.*, 1984; Kohno, 1984), although, doubts on its status as a scombroid were voiced (Collette, 1978; Collette *et al.*, 1984; Gosline, 1968). *Gasterochisma* may not be a scombroid, but a convincing alternative systematic placement has not been proposed. Apart from apparent scombrid characters, *Gasterochisma* has some primitive traits. It possesses, for example, three small bones anterior to the origin of the first dorsal, while in scombroids there may be one such predorsal bone, only in some gempylids. Otherwise, the absence of predorsals is considered a scombroid synapomorphy. Johnson (1986) recorded as many characters as possible on *Gasterochisma* specimens. He found that *Gasterochisma* lacks several essential scombroid synapomorphies. Eventually, Johnson ran his analysis without using the recorded data of *Gasterochisma*, stating that the characters, for which *Gasterochisma* has missing entries, have to be known for a proper understanding

of its relationships. However, a trial run of Johnson's data, including *Gasterochisma*, resulted in a monophyletic clade of Scombridae, which includes this controversial genus (see §2.3). Molecular phylogenetic analyses of Block *et al.* (1993) and Finnerty & Block (1995) result in *Gasterochisma* being a scombroid. However, I have little confidence that those cladograms represent the evolution of scombroids (see §2.4). Based on the absence of certain apomorphies, I would be ready to accept that *Gasterochisma* is not a scombroid. It is therefore puzzling to see it appear within scombroid clades in cladistic analyses. Characters that seem to unite *Gasterochisma* and scombroids, as mentioned at the start of this section, are not unique to scombroids, since caudal fins covering their bony support and a non-protrusible upper jaw occur in *Luvarus*. I follow for now the general concesus that *Gasterochisma* is a scombrid, taking into account that it appears in a Scombroidei clade after cladistic analyses. However, I suspect that *Gasterochisma* is not a scombroid. Hopefully the new character analysis, presented in this thesis, will provide a clearer picture of the evolution of some characters, and therefore also of the relationship of *Gasterochisma* to (other) scombroids.

A definitive systematic partition of scombroids cannot be offered before my results are given and discussed. As a starting point, I use Collette *et al.*'s (1984) division of scombroids. Notable (sub-)divisions within scombroids are made by Schultz (1987, see below) and Kishinouye (1923, see § 1.4).

Schultz (1987) proposes a subdivision of billfishes, mainly based on rostral characters. Acknowledging that there are many differences among the rostra of the different billfishes, I tend to agree that rostra provide good taxonomic characters, but I do not think that all subdivisions quoted by Schultz are valid. His conclusions are based on a small set of specimens. Based on this, I agree with Fierstine & Voigt (1996) who claim that Schultz's Tetrapturidae should be regarded as Istiophoridae and that *Pseudohistiophorus* de Buen, 1950 re-established by Schultz, is a *Tetrapturus*. *Thalattorhynchus* Schultz, 1987 is based on a fossil rostrum. The assignment of this "new" genus is primarily based on the eccentrically-placed nutrient canal, an anomaly previously found in Istiophorids. I have seen rostra of Recent *Tetrapturus*, in which the cross-section close to the apex shows just one of the normally two lateral nutrient canals. Although I do agree that billfish can be identified based on isolated rostral remains (see Fierstine & Voigt, 1996 for an identification method based on rostrum morphometrics and Fierstine & Voigt, (1996); Fierstine *et al.* (1997); Fierstine (1998, 1999) for the implemetation), I do not think that taxonomic subdivisions can be made based solely or mainly on rostral characters. It would be wrong to undervalue or ignore the numerous post-rostral characters.

1.4 The tunas

"What is the difference between a fish and a piano?"
"You can't tune a fish."
(Well known children's joke, origin unknown)

Kishinouye (1923) established a new order of Plecostei, which includes all tunas. These Plecostei are supposed to be closely related to the teleosts, being a sistergroup to the scombroids *sensu* Kishinouye (1923) (scombrids *sensu* Collette *et al.*, 1984 minus thunnini). This order is based on characteristics related to endothermy (mainly the subcutaneous vascular system, which is closely associated with the internally placed red myotome muscle, see § 4.1). Kishinouye (1923) failed to see the relationship between this subcutaneous system and a high metabolism. A subcutaneous vascular system, related to endothermy, is no grounds for creating a whole new order. It seems that the characteristics that Kishinouye (1923) thought to be unique are merely adaptations to a higher metabolism, which can be explained within the framework of Teleostei, without the need for creating a new order. Another endothermic fish group are the lamnid sharks (Carey, 1966 and 1973; Carey *et al*, 1971). Despite their anatomical adaptations to endothermy, similar to those of tunas, their status as sharks has never been in doubt. Takahashi (1924) concludes that the anatomical conditions Kishinouye had thought to be unique to the "Plecostei" are not unique to these at all. Takahashi (1924) is still uncertain whether vascular plexuses, found in the "Plecostei" are unique to those fishes or whether they are also found in "teleosts". It is known, however, that similar plexuses of intertwined capillary bloodvessels are found in many teleosts, where they play a role in gas exchange between blood and the swimbladder. The vascular plexuses that Kishinouye (1923) and Takahashi (1924) are concerned with are the primary structures responsible for the scombroids' endothermy (see § 4.1). Takahashi (1924) states that the occurrence of these plexuses is not equal in weight to those characters that differentiate the orders of Teleostomi. The forming of these plexuses is a subtle adaptation for a higher metabolism, rather than a radical new development. I follow here Takahashi (1924) and all subsequent authors, who retain the tunas within the teleosts. Kishinouye (1923) furthermore subdivides the Plecostei into families such as Katsuwonidae and Thunnidae. He also identified many new species, amongst others in the genus *Thunnus*. I view most of these as invalid, because the differences among all the species he quotes seem to be too small and insignificant (see Kishinouye, 1923). One could at most identify two *Thunnus*-groups, but not the several species which Kishinouye suggests. Only *Thunnus obesus* (Lowe, 1839) the bigeye tuna, does not seem to fit well into either of the groups. Kishinouye's (1923) tuna systematics are mostly

rejected (Gibbs & Collette, 1967; Collette, 1978). The only one of the new taxa Kishinouye (1923) erected which is still recognised is *Katsuwonus*.

Collette (1978) subdivided *Thunnus* into two groups, based on Kishinouye's data, thus creating two subgenera: *Neothunnus* Kishinouye, 1923 and *Thunnus* South, 1845. Collette's (1978) *Neothunnus*, or the yellowfin group, contains *Thunnus atlanticus* Lesson, 1831, *T. tonggol* Bleeker, 1851 and *T. albacares* (Bonaterre, 1788). Collette's (1978) *Thunnus*, or the bluefin group, contains *T. thynnus* (Linnaeus, 1758), *T. alalunga* (Bonaterre, 1788), *T. maccoyii* De Castelnau, 1872 and the "aberrant" species *T. obesus*. Later, Collette (1999) suggests to reinstate *Thunnus orientalis* Temminck & Schlegel, 1844 as a valid species. *T. orientalis* is mostly known as a subspecies of *T. thynnus*. Collette's (1978) subdivion of *Thunnus* is a different appoach from that of Le Gall *et al.* (1975) who established three subgenera, with the divergent *T. obesus* in a monotypic subgenus *Parathunnus* Kishinouye, 1923. The main difference among the two groups as in Collette (1978) is the anatomy of their heating organs, which differ substantially among the members of different groups (see also § 4.1). The main reason for Collette to include the apparently anomalous *T. obesus* in the bluefin group is that the stucture of its heater organ fits perfectly in this group. The two different types of heater systems in tunas represent two different adaptive strategies (Collette, 1978 and § 4.1, this thesis). However, there is evidence that contradicts this subdivision of *Thunnus*. Allozyme data from Elliott & Ward (1995) (WAGNER trees) and mtDNA data from Alvarado Bremer *et al.* (1997) (Neighbour-joining data) suggest that *T. obesus* is more closely related to yellowfin *Thunnus* than to the bluefins. Alvarado Bremer *et al.* (1997) also suggest that the two *T. Thynnus* subspecies, *thynnus* Linnaeus, 1758 (Atlantic northern bluefin) and *orientalis* (Pacific northern bluefin), are very divergent, as the mtDNA of *orientalis* is much more similar to that of the albacore (*T. alalunga*) than that of its Atlantic counterpart. Moreover, RFLP (restriction-fragment-length polymorphism) analyses of the nuclear ITS1 region (Chow & Kishino, 1995) suggest that the albacore is highly divergent from all other tunas. An explanation for the extraordinary "relationship" among the Pacific northern bluefin and the albacore is that introgression of albacore mtDNA into *T. t. orientalis* populations occurred while there was a barrier for introgression at the level of nuclear DNA (Chow & Kishino, 1995), while there was more free flow in mtDNA. Another theory is that *T. alalunga* and *T. t. orientalis* retained ancient mtDNA lineages while mtDNA of other tunas differentiated (Alvarado Bremer *et al.*, 1997). A mentioned above, Collette (1999) argued that *T. orientalis* is a valid species on its own. Collette (1999) concluded that the subspecific differences between *T. t. thynnus* and *T. t. orientalis* are really specific differences, supported by the above mentioned molecular data. It should also be mentioned that support for monophly

of the bluefin tunas on the basis of mtDNA control region-data (Alvarado Bremer *et al.*, 1997) is not strong (bootstrap values of 69, 79 and 88 % are given in their different analyses). All this indicates that there is a need for thorough research on the status and systematics of these tunas, in order to obtain robust results. It is hoped at this point that inclusion of extinct tunas in the phylogenetic analysis can provide new data leading to robust results. However, because I had to limit my study of the tunas, the results to be presented in this thesis might not solve these questions at this point.

1.5. Choice of outgroup taxa

In Table 1.1 I have already presented a list of outgroup taxa. Some of these taxa have been highlighted in § 1.3. There are various reasons for choosing the different outgroup taxa, discussed below. All outgroup taxa come from within the Perciformes, the order to which the scombroids belong.

Coryphaena. This perciform fish was chosen, since there are some superficial resemblances among coryphaenids, scombrids and billfishes. A coryphaenid has roughly the same body outline and streamline as an istiophorid. The shape of the caudal peduncle and the tail fin of a coryphaenid are very similar to those of scombrids and billfish. It is probable then, that these are adaptations towards similar swimming methods. The inclusion of coryphaenids in outgroups is hoped to provide clues to whether some morphological features in different groups are independent acquisitions, indicating parallel adaptations for the same condition, or whether they indicate phylogenetic relationships. Later, remarkable similarities among coryphaenids and fossil billfish have been found (Chapters 5, 7 and 8), making the inclusion of *Coryphaena* as an outgroup taxon most interesting. It has been used as an outgroup taxon in molecular phylogenetic analyses of scombroids (Block *et al.*, 1993; Finnerty & Block, 1995).

Trachurus. This carangid genus was chosen because it is a seemingly plesiomorphous (with regard to scombroids) percoid fish. *Trachurus* possesses, for example plesiomorphous traits such as a protrusible premaxilla and predorsal bones (see also Chapter 5). Previously; carangids were thought to be part of scombroids (see Bannikov, 1987). The osteology of *Trachurus* has been very well described by Suda (1996).

Luvarus has long been considered a scombroid but is now placed in the acanthuroids (see also § 1.3). Luvarids are plesiomorphous with regard to the scombroids (for example in gill arch characters), but they do possess traits which are also considered scombroid synapomorphies. Not only does their relative primitiveness make them a good outgroup, it is hoped that their inclusion as an

outgroup could shed some light on parallel evolution of certain traits. Are all scombroid synapomorphies valid synapomorphies, or has homoplasy led to incorrect conclusions on phylogenetic relationships?

Scombrolabrax. This taxon has until recently been considered a scombroid. Despite the similarities among scombroids and *Scombrolabrax*, it is a perciform fish which is plesiomorphous with regard to scombroids (see also § 1.3) and therefore ideal as an outgroup taxon. Collette *et al.* (1984) and Johnson (1986) have included *Scombrolabrax* in their analyses as an outgroup taxon; in Collette *et al.* (1984) it was the only outgroup taxon.

"Mugilidae". The mullets *Mugil*, *Liza* and *Valamugil* have been studied under the single denominator "Mugilidae" (in quotation marks, because not all mugilids are included). The aim of including these perciform fishes was the hope for clarity regarding the position of *Sphyraena*. As outlined in § 1.3, *Sphyraena* is thought to be either related to the mugilids or considered a scombroid.

Sphyraena. Barracudas will be, in different analyses, included as either an ingroup or outgroup. Inclusion of mugilids should bring some clarity regarding the position of *Sphyraena*.

CHAPTER 2: IMPLICATIONS AND ACCURACY OF PREVIOUS STUDIES

2.1 Introduction

The most important controversies on the systematics of the scombroids are highlighted below.

The two most recent cladograms based on morphological analyses were constructed by Collette *et al.* (1984) and by Johnson (1986). Their results show some major differences. The systematic divisions applied by both differ. Johnson's (1986) Scombroidei is equivalent to Collette *et al.*'s (1984) Scombroidei+*Sphyraena*-Gasterochismatinae. There are many differences in both cladograms throughout, but the position of the billfishes is the most striking controversy (see Figs. 2.1-4). The differences among the morphological cladograms are summarised in Fig. 2.3. The Lepidocybiinae are not included with Johnson's "Gempylinae" (snake mackerels) but are considered a sistergroup to the Trichiuridae (cutlassfishes) and the "other snake mackerels". Johnson suspects Gempylinae to be a paraphyletic group that needs further study. In Collette *et al.* (1984) the trichiurids and gempylids are not closely related. Johnson (1986) puts the "Gempylinae", Lepidocybiinae and Trichiurinae in one Gempylidae-clade. *Gasterochisma* might belong to Johnson's Scombridae, but he considers their position still *incertae sedis*. Collette *et al.* (1984) place *Gasterochisma* in a monotypic subfamily Gasterochismatinae, thus placing the rest of the scombrids in the paraphyletic subfamily Scombrinae (Fig. 2.1a). The Sardini and Thunnini, the most derived scombrids according to Collette *et al.*, are relatively plesiomorphous offshoots in Johnson's Scombridae. The most striking difference is the position of the Xiphiini and the Istiophorini (billfishes), the most apomorphous scombrids according to Johnson and one of the earliest scombroid offshoots according to Collette *et al.*. There are also some agreements among the two views. Both views suggest that the Scombrini are the earliest scombrids. Uyeno & Fuji (1975) found the Scombrini are the most primitive scombrids, through a morphological analysis of scombroid caudal regions. It is also agreed that the Scomberomorini are amongst the most derived scombroids. There is disagreement on whether the tunas or the billfishes are the apomorphous sister group of the Scomberomorini

More recent cladograms were published by Block *et al.*, 1993 and Finnerty & Block (1994, 1995). Their phylogenetic analyses, based on molecular data, seem to suggest two things: *Gasterochisma* does belong to the scombrids, and the billfishes are distantly related to the other scombroids or even a sister group to these (Finnerty & Block, 1995). These cladograms (Fig. 2.4), are based on analyses of the *cytochrome-b* gene. Finnerty & Block (1994, 1995) have added

more outgroups and the scombroid *Acanthocybium* (the wahoo) to the analysis of Block *et al.* (1993). Both cladograms contain paraphyletic and polyphyletic groups (Fig. 2.4, see also § 2.4). The results of the two different analyses are divergent enough to assume that the evolutionary history of the *cytochrome-b* gene in scombroids is not presented in robust cladograms, and that the trees for these genes are probably not congruent with the species tree. The molecular data seem thus to produce fragile results. Further evidence for this is given in § 2.4. According to Nelson (1984, 1994) *Acanthocybium* is to be included under the Scomberomorini. Finnerty & Block (1994, 1995) thus make this tribe (*sensu* Nelson, 1994) paraphyletic within an already paraphyletic family of scombrids. The greatest implication of Finnerty and Block's result is that the billfishes are not scombroids, but a sister group of *Sphyraena*, *Coryphaena* and the Scombroidei (see Fig. 2.4b).

Other systematic divisions are made by Schultz (1987), who recently revised billfish systematics on the basis of rostral characters. Schultz (1987) resurrected the Tetrapturidae for part of the istiophorids, but this division is rejected by subsequent authors (see also § 1.3). Fossil scombroids are extensively treated by Casier (1966) and Bannikov (1985).

Data about the interrelationships and the evolution of solely Recent scombroids have already been published. I highlighted before (see Introduction) what the differences among the results of recent phylogenetic analyses are. Here I will show in detail what each of these studies implies. Moreover, the emphasis in this chapter is less on the evolution the cladograms express, and more on a critical look at how these cladograms are produced and the statistical indices that go with those respective cladograms. These aspects of the cladogram can be used as tools to assess the reliability of the proposed evolutionary hypotheses, in terms of the hierarchical information content of the data on which the cladograms are based.

The material consists of the data files from which the published phylogenies are constructed (Collette et al., 1984; Johnson, 1986; Block et al., 1993 and Finnerty & Block, 1995). The extraction of Collette et al's data file caused some problems, as will be shown below. These data matrices were initially re-run in PAUP version 3.1.1 (Swofford, 1993), to determine the accuracy of the presented data. Collette *et al.*'s (1984) data were at a later stage re-run with a new test version of PAUP (Swofford, 2000) The topologies and tree statistics of the trees thus obtained are compared with the previously published results. The data set that was the basis for the trees in Finnerty and Block (1994, 1995) had also been subject to AutoDecay, version 3.0.2 (Eriksson & Wikström, 1996) to calculate the decay indices (Bremer support values).

2.2 Re-analysis of Collette *et al.*'s data

The data provided by Collette *et al.* (1984) can be used for a re-run of the analyses. However, the data matrix is not published, but only a description of the character coding (Collette *et al.*, 1984, appendix). The plesiomorphous condition, in Collette *et al.* (1984), state 0 for every character, is the condition as present in *Scombrolabrax*. In the cladogram (Collette *et al.*, 1984, Fig. 312), character state changes (progressive evolution, reversals, homoplasies) are indicated, so for all OTUS in the cladogram, all character states could be retraced, to re-create Collette *et al.*'s (hypothetical) data matrix. The result of this retracing work (Table 2.1) is however not fully unambiguous. The evolution of characters 20 and 38, as mapped on their cladogram is ambiguous. If I interpret Collette *et al*'s cladogram right,

Table 2.1. Possible data matrix of Collette et al. (1984). For character coding, see Collette *et al.* (1984, appendix).

Format equate="A={01} B={12}"	
	[00000000011111111122222222233333333334]
	[12345678901234567890123456789012345678901]
Scombrolabrax	01010000000000001000000000100000000210
Trichiuridae	11000000010000001101000000200000000100
Gempylidae	100000100A100010011A00000001B01B11111B00
Xiphiidae	11101100111011000010000000010101111111010
Istiophoridae	11101100110111000010000000010111211100020
Scomber	11110010110101000010000000011111110100020
Rastrelliger	11110010110101000010000000011111110100020
Gasterochisma	0000?01101010100001000000001211110100020
Grammatorcynus	11000010011101000010000000011111110100030
Scomberomorus	11101011011101000010000010012111111110030
Acanthocybium	11101111011101000010000010012111111110030
Orcynopsis	11101011011101000010000000012111211110031
Cybiosarda	11101011011101010010010000012111211110031
Sarda	11101011011101010010010000012111211110030
Gymnosarda	11101011011101010010010000012111211110030
Allothunnus	11101011011101010010010001012111211110030
Auxis	11101011011101011010011001112111211110030
Euthynnus	11101011011101011010011101112111211110040
Katsuwonus	11101011011101011010011101112111211110040
Thunnus	11101111011101011010011101112111211110050

within gempylids character 20 progressed from state 0 to 1, only to reverse back to state 0 within that group. From the cladogram alone it is not clear at which node within the gempylids the progressive evolution took place and at which node the subsequent reversal, which could make the state of character 20 in every node above the gempylids ambiguous. Collette *et al.*'s character 20 is: number of ossifications in last dorsal and anal pterygiophores (see Chapter 5, osteological descriptions) one (0) or two (1). This must refer to the fact that some gempylids have pterygiophores which are formed from two ossifications, whereas in other scombroids this stay originates from a single ossification (Collette *et al.*, 1984: table 166 and 161; Potthoff *et al.*, 1986). I have thus proceeded to code state A for character 20 in the gempylids in Table 2.1 and 0 elsewhere. The apomorphous or plesiomorphous state of each character can be derived from the fact that in Collette *et al.* (1984) the *Scombrolabrax* state is considered plesiomorphous and any progressive state change gives an apomorphous state. Also, the order in which the character states are mentioned in Collette *et al.*'s (1984) character list goes from plesiomorphous to apomorphous (Johnson, 1986). Still, if a data matrix is to be reconstructed, it is not certain whether the character coding used is similar as the one used by Collette and his co-workers. In their cladogram it is not indicated whether certain clades or OTUS contain missing entries in the character matrix. In their cladogram, Collette *et al.* (1984, fig. 312) do not indicate the individual genera of gempylids they studied, but figure a paraphyletic group indicated as Gempylidae. I have attempted to reconstruct the character states for this paraphyletic collective (Table 2.1). However, elsewhere Collette *et al.* (1984, fig. 314) accept without question the monophyly of gempylids based on Russo (1983). Johnson (1986) questions certain aspects of the methodologies of Collette and his co-workers. Johnson criticises their interpretation of certain homologies (e.g. gill filament cross-connections) and distribution of certain character states (e.g. vertebral number), which he reports to be incorrectly indicated on Collette *et al*'s cladogram. Collette *et al.*'s cladogram was constructed using WAGNER 78. I have constructed a hypothetical data matrix (Table 2.1) of Collette *et al.*'s data and had PAUP construct consensus trees. I used a heuristic search with a simple addition sequence. This addition sequence to construct starting trees is the WAGNER method as proposed by Farris (1970). According to the WAGNER method, all characters (including multistate characters) are treated as unordered. Branch swapping has been performed. None of the consensus trees retrieved from this re-analysis conforms with Collette *et al.*'s cladogram. The combinable components ("semistrict") trees of the matrix from Table 2.1 thus obtained is in Fig. 2.1b. In that tree, the taxa *Gasterochisma*, *Grammatorcynus*, the paraphyletic Scomberomorini (without *Grammatorcynus*), billfishes and Scombrini form an

unresolved bush. The fragility of the data is also demonstrated by the fact that the majority of nodes (Fig. 2.1a) is not well supported (i.e. with a bootstrap value of <95%). It is remarkable though, that the node above the trichiurids seems to be the most strongly supported (Fig. 2.1a). Johnson (1986) considers "Trichiurinae" to be specialised gempylids and finds Collette *et al*'s placement of trichiurids as sister group all other scombroids "perplexing". According to Collette (pers. comm., 1997) the original data matrix of this analysis does not exist any longer.

2.3 Re-analysis of Johnson's data

Johnson (1986) did not include *Gasterochisma* in his eventual analysis, although he coded the characters of this genus, as far as they were known He stated that this taxon, showing a remarkable combination of primitive and derived characters, needs to be studied before assigning a definite systematic place to it. Based on Johnson's initial data I have created two cladograms: one in which *Gasterochisma* is included in the analysis and one where it is excluded. The analysis with *Gasterochisma* resulted in a cladogram with *Gasterochisma* as the most primitive member of Johnson's scombrids. The rest of the topology of the tree I thus obtained is the same as Johnson's phylogeny. When excluding *Gasterochisma*, the topology of the Scombroidei-branch of my analysis is the same as in Johnson's (Johnson, 1986). The topology of the outgroups differs for Johnson's and my cladograms, but I do not consider this a topic for discussion. Johnson (1986) indicated that changes in the phyletic sequence of the outgroup did not affect his hypotheses of character polarity for the analysis of the relationships within his in-group. However, his data are quite fragile and not many nodes are greatly supported by bootstrap replicates (Fig. 2.2a). Carpenter *et al.* (1995) presented a revised version of Johnson's data matrix. As a result of this revision, some of the entries in Johnson's data matrix are revised, some characters are reinterpreted. Seven characters that apply to the monophyly of Sardini and Thunnini in Collette *et al.* (1984) are introduced and five new characters are introduced based on new evidence found by Carpenter *et al.* (1995). When I used this updated data set, it resulted in a tree in which only the position of *Gasterochisma* has been altered (Fig. 2.2b). The topology of the rest of the tree remains the same. Carpenter *et al.* (1995, fig. 3) produced a less resolved tree with a tree of a length of 85 as opposed to my tree of 84 steps. Carpenter *et al.* (1995) used HENNIG86 for their analysis, which might explain this difference.

2.4 Re-analysis of Block *et al.*'s data

The data that Block *et al.* (1993) and Finnerty & Block (1995) used are reliable, but the presentation of it in publications and on the internet is not. The following paragraphs deal with these data, provided from original data matrices, GenBank and published data matrices, and the results I obtained after cladistic analyses of these data, which led to the above statement.

Block *et al.* (1993) give a good description of their methods in PAUP. I have copied their published data matrix methods exactly in my analyses. However, preplexingly, their results are different from mine (Fig. 2.4c). One essential difference is to be found in *Sarda*. In Block *et al.*'s analysis the two *Sarda* species are one clade, whereas in my execution of their data set, *Sarda* appears to be divided over different clades. *Sarda chiliensis* Cuvier, 1832 is in a clade with tunas and *Sarda sarda* (Bloch, 1793) forms a clade with *Auxis thazard* (Lacépède, 1800). This does not only create non-monophyletic groups, but also mixes up groups which are considered endothermic and exothermic (Fig. 2.4c). This is why I suspect that the numbers to indicate the taxa in their data matrix contain some errors. In my analysis, taxa 16 and 17 are always found together as one clade; this could very well be the *Sarda*-clade. This would mean that Block *et al.*'s taxon 17 is not *Auxis thazard*, but one of the *Sarda*, supposedly *Sarda chiliensis*. Number 16 would then be correctly assigned to *Sarda sarda* by Block *et al.* in 1993. Taxon 15, in my cladogram in one clade with tunas, should then refer to *Auxis thazard* instead of *Sarda chiliensis*, as Block *et al.* do. Even then, there are more differences among their analyses and mine (compare Figs. 2.4a-c). There are also some statistical differences. For example: the two MPT's I obtain (contrary to Block *et al.*'s one MPT) are 1311 steps and the number of informative characters is 228, compared to 1292 steps and 218 informative characters in Block *et al.* (1993). It is puzzling why my results should differ from mine. Is there a difference between the published and the actual data matrix, or is the methodology not well reported?

At a later stage, Finnerty & Block (1995) published another cladogram based on data which are also contained in Block *et al.* (1993). I downloaded the aligned scombroid sequences deposited in GenBank, which supply the data for the 1995 cladogram. I subsequently ran the same PAUP analyses as described in Finnerty & Block (1995), using those data. The results are again different and for sure impossible clades are formed (not figured). It transpired that the sequences in GenBank differ from the data matrix published in Finnerty & Block (1995). Finnerty allowed me to work with the original data files and then the results from the analyses are not different from the ones that he proposed. The sequences in Genbank were at the moment of my investigations (1997) clearly inaccurate and misleading. It must be mentioned that shorter trees than the one published in

Finnerty & Block (1995) can be found with these data. Finnerty (pers. comm., 1997) admitted that this had been found after the publication in 1995. The shortest tree found, 2218 compared to 2224 steps[3] (Fig. 2.4d) implies paraphyly of the tunas. This would require other scenarios of evolution of scombroid endothermy then postulated before. There is more to be mentioned regarding the length of the trees. When a constraint is enforced which results in a tree with the topology as in Finnerty & Block (1995, fig. 4) the two MPT's are even shorter than the unpublished tree of 2218 steps, namely 2215 steps. Further analyses with constraints proved that there are much shorter trees, the shortest to be found so far are not longer than 2209 steps (Not figured. These shorter trees include clades that make groups, generally accepted as monophyletic, paraphyletic). The fact that there are much shorter trees is expressed as well by the decay indices (Bremer support values) in Fig. 2.4b.

Although the original data file gives trees which correspond with the published ones, it is not a very robust one. The majority of the nodes is not greatly supported by bootstrap replicates (Fig. 2.4b).

2.5 Discussion and conclusions

There are differences found among the phylogenies already published and the cladograms I have obtained after executing the (possible) detests in PAUP. I have repeatedly cross-checked the published data and the ones I used for errors and many times considered the tree-constructing methodologies as published, seeking to repeat the phylogenetic analyses exactly according to the original tests. I also executed a particular data set more than once. I am thus confident of the results that I present here. This raises some doubts about whether any of the published data sets is reliable. None the of the data presented seem to be robust. For example, small changes in the correct molecular data matrix caused disproportionally large changes in the resulting trees. Low bootstrap values for all three data sets underline the fragility of the data. Of all the data sets discussed, only Johnson's (1986) data matrix gives exactly the same cladogram as the one published by the author(s).

There are notable differences between Collette *et al.*'s (1984) tree and mine. Collette *et al.* probably focused more on an "overall similarity-approach" than I did, knowing they have used WAGNER 78 for their analysis, which I think accentuates less the evolutionary process than PAUP does, thus explaining the differences between their tree and mine. I prefer a parsimony approach. Another reason for

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[3] Finnerty & Block (1995) mention a shortest tree of 2348 steps, as this was the output of their tree file. This tree was in fact 2224 steps long. PAUP appears to malfunction when asked to describe the length of a saved tree when a character weights' stepmatrix is used which is internally inconsistent. This stepmatrix might be internally inconsistent, but the values represented in it are correct nonetheless. This is an exceptional case.

these differences could be that the data matrix I used in the analysis was eventually not the same as theirs. Fortunately, nowadays the good practice of providing the data matrix in papers is upheld.

The analysis of Johnson (1986) agrees with mine, but I should point out that Carpenter *et al.* (1995) discovered some weaknesses in Johnson's data. The difference in ranking of *Gasterochisma* in Johnson (1986) and Carpenter *et al.* (1995) shows how difficult it is to place this enigmatic genus.

Tuna paraphyly is, with Finerty & Block's (1995) data set, attained when a weighting scheme is applied which emphasises more the phylogenetic signal from slowly evolving base-substitutions, compared to the unweighted analysis. In the latter, tuna monophyly is evident, although poorly supported by bootstrap-values: less than 50% (Block *et al.*, 1993; Finnerty & Block, 1995). The "break up" of the tunas in the weighted analysis is explainable through the probably recent speciation of all tuna species. Chow & Kishino's (1995) mtDNA data prove that the earliest offshoot of *Thunnus* is the albacore (~2 Mya) and most *Thunnus* differentated ~500,000 years ago. Although *cytochrome-b* thus provides no hard evidence against tuna monophyly, it must be taken into consideration because of the far-reaching evolutionary consequences.

I firmly believe that to solve these problems, there is a need to continue the investigations into the systematics of the Scombroidei. My contribution in what is hoped to be a series of efforts to solve these problems is including the fossil taxa and using novel techniques for constructing cladograms, such as those of Wilkinson (1995) and Wilkinson & Benton (1995, 1996), as mentioned earlier (see also § 8.3).

CHAPTER 3: COMBINING RECENT AND FOSSIL EVIDENCE-A SHORT BACKGROUND

3.1. Introduction

The main aim of the work presented here is a phylogenetic analysis in which fossil and Recent evidence is combined. Is that a valid approach? Can one put fossil data on a par with neontological evidence? Are the fossils not too disadvantaged since so much more is known about the Recent taxa? Today, the census seems to be that it is acceptable to most to combine fossil and Recent evidence, arguing that the new combinations of characters of fossils can provide new information on relationships of Recent taxa (Donoghue *et al.*, 1989; Smith, 1994). However, some still cast doubt on the usefulness of fossils in cladistic analyses with Recent taxa (Patterson, 1998; Johnson and Collette, pers. comm., 1998). Below I will highlight both sides of the argument.

3.2. Arguments against combined analyses

Willi Hennig, considered the founder of phylogenetic systematics, stated that fossils are useful to detect convergence in a phylogeny, but can never be treated as equal to Recent taxa due to incompleteness Hennig (1966). Hence, they can only be put in the cladogram after the analysis, at the stem-groups. The most avid opponent against inclusion of fossils was arguably Patterson (1981), who stated that pre-Darwinian workers wanted to know how fossils are related to extant taxa, not how Recent taxa are related through fossils and he praised them for that. However, I see little difference between the two statements. Patterson supported his claims, showing that there were no known phylogenetic analyses in which fossils have managed to overturn known theories on relationships. Patterson suggested a similar role for fossils as Hennig did: use information of their age, palaeobiogeography and new combinations of characters, which, however rarely, can help one decide on issues on homology and character polarity.

3.3. Arguments in favour of combined analyses

My personal argument for including fossil taxa in a cladistic hypothesis such as the one presented in this thesis are the following. I consider fossil taxa as extinct life forms. The fact that they are extinct does not make them much different from extant taxa, certainly if there is still material available for research. To wilfully exclude them from cladistic analyses would be foolish. Because of the different

character combinations that the fossils have, their inclusion in a cladistic analysis might change the topology of the cladogram. Even if they do not alter tree topology, fossils can provide vital information on character evolution. Fossils are the only evidence of biological history that is long past. Do the merits of fossils outweigh the disadvantages mentioned in § 3.1? Evidence provided by combined analyses are mentioned below.

3.4. Evidence of combined analyses

Patterson (1981) argued that there are no known instances in which fossil taxa managed to overturn existing phylogenies of Recent taxa. However, a few years later positive evidence appeared that supports the usefulness of fossils in a combined analysis.

Doyle & Donoghue (1987) included fossils in their analysis of seed plants and found that tree topologies were not influenced, but new insights in character evolution are achieved. Gauthier *et al.* (1988) found that the inclusion of fossils in their analysis of amniotes, has overturned the tree topology. More recently, phylogenetic research of fossil and Recent arthropods (Wheeler, 1993; Wills *et al.*, 1998; Schram & Hof, 1998; Hof, 1998) has also produced significant results. They show that the inclusion of fossils can refute some existing hypotheses of relationships. In those analyses, the fossils were found to be essential or at least positive contributors.

3.5. Discussion

It seems that, when done properly, the disadvantages of including fossils in analyses are outweighed by their advantages. If a fossil lacks much information, it does not necessarily mean it should be excluded. Maybe the information that the fossil does hold is crucial while some Recent taxa hold no vital information at all (see Wheeler *et al*'s, 1993 explanation for including Trilobita in their arthropod phylogeny). However, There should be balance between two extremes: fossils reveal nothing, or fossils will reveal all. Fossils have their use but will never reveal all because of their missing data (Smith, 1994).

One could think that taxa, in which soft-body parts play a major role in taxonomy, would be less fit for combined Recent/fossil analyses than those whose taxonomy depends mainly on hard body parts, such as arthropods. The most important taxonomic features of arthropods fossilise well. However, The results of

amniote phylogeny (Gauthier *et al.*, 1988) and teleost phylogeny (see Arratia, 1998) show that fossils of these taxa have their usefulness.

CHAPTER 4: ENDOTHERMY

4.1 Introduction to scombroid endothermy

Fishes are generally regarded to be ectothermic animals. Exceptions to the rule are tunas (except maybe *Allothunnus*, see below) and mackerel sharks (Lamnidae), which conserve heat in swimming muscles (Carey & Teal 1966; Carey *et al.*, 1971). Tunas also possess tissues that provide brain and eye heating (Linthicum & Carey, 1972), which is the only system of body-warming that the billfishes and *Gasterochisma* have (Carey, 1982). The brain and retina of *Gasterochisma* and the billfishes are endothermic while the body is ectothermic (cranial endothermy). Alexander (1996) suggested that there is also cranial endothermy in mobulid rays. Other scombroids are fully ectothermic.

Endothermy is a special feature in fishes, a conspicuous apomorphy rarely found in these animals. This makes it an interesting aspect of the phylogenetic analyses of scombroids, especially since there are three distinct groups in which this trait is found. Selective advantages of either whole-body endothermy (systemic endothermy) and the cranial variety is that these fishes are better capable of constant swimming, acceleration and diving fast into the colder depths of the water, especially so since these fishes are predators.

In Recent specimens, endothermy can be inferred by the histology of their myotomes (Fig. 4.1). Most of the muscle tissue in a fish myomere is white muscle, but red muscle is also mostly present. Most ectothermic fishes have in their myotomes a patch of red muscle only near the skin (this is **character 74, state 0** in Appendix 3, see Fig. 4.1c). The Sardini, always considered to be the ectothermic fish most closely related to Thunnini, have a patch of red muscle in the middle between the outer margin of the myomere and the vertebral column (**character 74, state 1**). The tunas and the lamnid sharks have a large patch of red muscle surrounding the vertebral column (Fig. 4.1a, b). This patch of red muscle stretches laterally to almost the outer margin of the myotome and is surrounded by white muscle tissue. This is **character 74, state 2** in Appendix 3. The position of the red muscle in the myotomes is Graham & Dickson's (2000) "new character 2". In the billfishes and *Gasterochisma* endothermy can be seen through the reddish brown tissues associated with eyes and brain (Carey, 1982). The heater organs in billfishes and *Gasterochisma* seem to be derived from different muscles. In *Gasterochisma* it is derived from the lateral rectus muscle (this is **character 77, state 1** in Appendix 3). In billfishes, it is derived from the superior rectus muscle (**character 77, state 2** in Appendix 3). Red muscles generate body heat. In most fishes this heat is quickly lost to the water, but in the endothermic scombroids the dark muscle is surrounded by *retia mirabilia*, "miracle networks", which consist of

closely intertwined counter-current arteries and veins, through which blood flow ensures that the body and/or the brain is constantly warmed and metabolic heat, generated as a result of muscular activity, is not lost to the surrounding water (Carey & Teal, 1966; Carey, 1982). There are two types of systemic heating systems used by tunas: one in which there are two relatively large heat exchangers at the lateral sides of the dark myotome-muscles and one in which the lateral heat exchangers are relatively smaller and there is a heat exchanger present just ventral of the vertebral column (Fig. 4.1b). Since the first mentioned heating system occurs in the subgenus *Thunnus sensu* Collette (1978), I call this the thunnoid heat exchange-system (**character 77, state 4** in Appendix 3) and the one with the central heat exchanger, occurring in *Neothunnus sensu* Collette (1978), *Katsuwonus*, *Euthynnus* and *Auxis*, the neothunnoid heat exchange-system (**character 77, state 3** in Appendix 3). Those with the thunnoid (bluefin tunas) system inhabit temperate waters, whereas the smaller tunas, with the neothunnoid system (yellowfin tunas) inhabit tropical waters (Collette & Nauen, 1983). The loss[4] of the central heat exchanger with the bluefins is more than compensated for by the great efficiency of the two lateral heat exchangers, which permits them to thrive in these cooler waters. The primitive tuna *Allothunnus* has a central vascular plexus of *rete mirabile*. It is suspected (Graham & Dickson, 2000) that this plexus is too small to be a heat exchanger providing for a high body temperature. However, it is not known if *Allothunnus* is endothermic or ectothermic, because field tests of its body temperature have not been done.

The internal placement of red muscle in tunas is not thought to be caused by endothermy. It is rather thought that this internal placement preceded the evolution of endothermy, because it has been proved that the association of dark muscle tissue with the vertebral column (dark muscle tissue and vertebral column are associated over the whole length of this tissue-patch, which is most of the length of the vertebral column) has to do with the thunniform (stiff-bodied) swimming mode of tunas. When a tuna swims, its body seems to be inflexible as it moves forward. There seems to be none or little lateral movement. The propelling force of the fish comes from the fast side-to-side movement of its tail. Billfishes, on the other hand, have a more undulatory form of carangiform swimming: as they move forward, there is a continuous undulation in the body, from the head to the tail, which causes the propelling force to move forward (Block *et al.*, 1993). The trichiurids, with their snake-like bodies have a form of swimming in which their body undulates with a great amplitude (Lindsey, 1978; Lighthill, 1969), the so-called anguilliform swimming mode. One can assume that the red muscle in trichiurids is not internalised, as is shown by pictures of a *Trichiurus* and *Evoxymetopon* in

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[4] Collette (1978) makes it evident that the neothunnoid form is the plesiomorphous condition, while the thunnoid system is more derived.

(Nakamura, 1994b, fig. 7c, d). Gempylids, with a carangiform swimming mode (Lighthill, 1969), which requires a flexible trunk, will not have internalised red muscle. This is also suggested by figures of *Gempylus* and *Thyrsites* in (Nakamura, 1994b, fig. 7a, b).

The phylogenies of scombroids based on molecular data (Block *et al.*, 1993; Finnerty & Block, 1994; 1995) give some insight into the evolution of endothermy. I have tried to see if traces of the heater organs can be found on the bones of the endothermic scombroids. This would surely be a great help for the examination of the fossil specimens.

4.2 Material and methods

A fresh tuna fish, nicknamed "Brenda" was, besides for the study of the tuna osteology (the skeleton is part of my small private collection), also used to see if evidence of heat exchangers can be found on the bones. To achieve this, pieces of flesh were sliced off the vertebral column and one of the eyes was removed to see if traces could be found in the eye socket. All these observations have been done with the naked eye. Subsequently, the fish was wholly defleshed as described above and traces were looked for with the help of a binocular microscope.

A paper by Bardet *et al.* (1993) explained that thin sections of fish bones can show if the organism in question has had a high metabolism. The bone, in their case, was a triangular one, supposed to have belonged to the branchial arch of †*Leedsichthys problematicus*, Woodward, 1889, an enigmatic gigantic fish of unknown affinities. I intended to pursue similar analyses with scombroid bones, but due to unforeseen circumstances this did not happen. It is hoped that this research will take place in the future.

4.3 Results

There were patches of red tissue surrounding the eye that formed the eye heater and caudal to the eyes, just rostral to the branchial cavity was a patch of dark red tissue. I cannot be certain that this dark tissue is the eye heater because I have not studied enough comparative material. As far as I saw then in the optical cavity there are no traces of these heating systems on the bones The brain and the eye are also surrounded by large amounts of fat tissue, which also have a role in conserving heat. Traces are also absent on the bones of the vertebral column and the ones associated with them. It is clear though that throughout most of the body the vertebral column is surrounded by dark muscles, being the centre of the myotome (Fig. 4.2). The rest of the myotome is light coloured.

The specimens of tunas I have seen so far indeed seemed to show some traces of blood vessels (see below) which are part of the heater system of these fishes. Ectothermic *Scomber* do not show these particular traces, nor do the skeletal remains of two salmons nicknamed "Enid" and "Jeffrey", which are part of my small private collection. These traces of blood vessels are however not so easy to trace.

The tuna specimens of my own private collection (see also specimen list, Appendix 1): three *Auxis* and one *Thunnus alalunga*, have been subject to a close examination in order to find possible evidence for heat exchangers. During this investigation I did not look for morphological adaptations as such (these are mentioned in § 5.2.2.4), but more for evidence of unusual concentrations of foramina and/or irregular grooves on the surface of the bones, which might indicate the presence of heat exchangers and "miracle networks". In the tuna specimens mentioned above, irregular shallow grooves have been found on the alisphenoid, the ventral side of the frontal and the sphenotic. The specimens of ectothermic fish in my own collection, two salmon and three mackerel, do not show these traces. Is it possible that these traces are indications of the eye and brain heaters as described by Linthicum & Carey (1972), who illustrate a paired heat exchange system of "miracle networks" located close to the brain? These *retia* are connected to the brain and eyes by relatively large blood vessels. It must be said, though, that the blood vessel-traces on my tuna specimens are not clear enough to state definite conclusions on what they are. The sphenotic, the frontals, the basisphenoid and the parasphenoid of my tuna also show a number of foramina through which the blood vessels might have ran. The alisphenoid, prootic and the parasphenoid show some conspicuous foramina, not seen in my mackerel and salmon. Are these foramina through which heat-exchanging blood vessels have ran? Unfortunately, that cannot be said. The results of this short investigation have been disappointing, in that what could be interpreted as evidence for endothermy in the cranial region is not obvious and clear-cut. On the contrary, the shallow irregular grooves observed are very faint and thin. The foramina mentioned above are not concentrated in certain patterns and their function is unclear. Investigation into this matter might be worthwhile, with more comparative material and careful dissections of fresh specimens.

Unfortunately, the vertebral column shows no evidence of a concentration of blood vessels connected to the centrally concentrated red muscles. However, there are clear morphological differences on the vertebral column, between tunas with a neothunnoid and a thunnoid heat exchange system (see § 5.2.2.4). These do not concern traces of blood vessels, but the macro-structure of parts of the vertebral column.

The traces and foramina, discussed above, have ultimately not played a role in the study of the fossils. The tuna-like †*Palaeothunnus* is preserved as a two-

dimensional fossil in the matrix. †*Eothynnus* has none of the above discussed traits preserved, even though three-dimensional skulls of these tuna-like (*sensu* Woodward, 1901; Casier, 1966) Eocene fish are known. Most fossil tuna remains that I have studied are isolated centra of vertebrae and a few parts of the caudal skeleton. None of the tuna fossils reveal anything regarding their body temperature or their metabolic rate. Morphological characteristics which are indications of either a thunnoid or a neothunnoid body warming strategy (see § 5.2.2.4) are not found in the fossils. Whether *Palaeothunnus* has any close relationship to the Thunnini or not, a fact is that it did not possess systemic endothermy, because it has no enlarged inferior foramina and neither does it have displaced haemal zygapophyses. Hopefully, in the future, histological analyses of fossil and Recent tuna bones can provide new insights into the evolution of tuna endothermy.

CHAPTER 5: DESCRIPTION OF CHARACTERS

5.1 Introduction

Here I present an extensive description of characters that are useful to identify, distinguish, and characterise scombroid fishes and the chosen outgroup taxa. Most of the characters described here are potentially phylogenetically relevant, but only some have survived it to the eventual list of characters that are used in the phylogenetic analysis. Explanations for exclusions of certain characters are given throughout the chapter. A schematic summary of the characters used in the phylogenetic analysis is given in Appendix 3. Because the analysis includes fossils, and the osteology of Recent scombroids is well known, I have focused on skeletal characters. However, the influence of soft-tissue anatomy on scombroid taxonomy cannot be ignored. Kishinouye (1923), for example, in his taxonomic revision of scombrids, extensively describes the soft-tissue anatomy. Regarding soft-tissue characters, I focus on external characters that seem to convey a clear phylogenetic signal, such as fleshy caudal keels or the position of the anus. Surely, beforehand, it was not known which characters are true synapomorphies, but some of the soft tissue characters used here are used to identify between different taxa. The fleshy caudal keels are found in only certain groups and only certain groups possess certain states of this character. The evolution of endothermy is an intriguing aspect of scombroid phylogenetic research (see § 4.1). Soft-tissue anatomy that evidences some endothermic capacity, such as the position of red muscle fibres in a myotome or a cranial heater system (a modified muscle), is also considered.

The characters I have chosen for my phylogenetic analyses are a mixture of those described in the literature and those which I now think to be relevant, but which have not been considered in detail, if at all. I have drawn primarily from characters as described in the two papers that treat the scombroids in general, Collette *et al.* (1984) and Johnson (1986). These two papers differ remarkably regarding the relevance of certain characters in phylogenetic research and the evolution of the characters themselves. Johnson described and presented many of the characters used in his 1986 paper in a conference in 1979. Many of these characters have been adopted by Collette *et al.* (1984) in their phylogenetic analysis. Yet, there are some obvious differences. There is, for example a larger number of gill arch characters in Johnson (1986) and a larger number of caudal region characters in Collette *et al.* (1984). The phylogenetic conclusions drawn in either paper differ remarkably (see also Chapter 2). A few of the differences in character use are discussed below.

Johnson (1986) criticised Collette *et al.* (1984) for overemphasising the caudal region characters. Johnson, however, is incorrect in his comments on separating the

pattern of fusion in caudal bones into the fusion pattern in the dorsal part and the ventral part of the caudal complex, as done by Collette *et al.* (1984). Johnson (1986) claims that fusion of elements in the dorsal and ventral part of the caudal complex always occurs simultaneously. However, this is contradicted by the gempylids, which show a great variety in the degree of fusion of the elements in the dorsal and ventral region of the tail bones. This was remarked before by Matsubara & Iwai (1958) and Russo (1983), and supported by own observations (see § 5.2.3.2). Thus, Fusion of elements in the dorsal half of the hypural plate is not always accompanied by fusion of ventral caudal elements (see § 5.2.3.2). While many of the other caudal characters employed by Collette *et al.* (1984) are not unique to scombroids (see for example § 5.2.3 for *Luvarus*), it would be wrong to dismiss this evidence, because clearly scombroids have undergone much evolution on a functionally morphological level in the tail region. While different traits might have developed for similar reasons (for example caudal fin rays strongly overlapping the supporting bones, and fusion of otherwise autogenous elements to create more rigidity), there is no evidence that these different traits are always correlated or have co-evolved. Studies by Uyeno & Fuji (1975) and Monsch (2000) show that combinations of caudal apomorphies are highly indicative of genera and are even useful to postulate phylogenetic hypotheses. Johnson (1986) on the other hand, puts much emphasis on the gill arch characters. However, if the importance of gill arch characters is appreciated, a problem arises when including fossils in the study. Gill arch characters are poorly fossilised. All of Johnson's (1986) gill arch characters concern aspects like the articulation of these thin and fragile bones and their associated cartilaginous and fleshy parts. Johnson (pers. comm., 1998) questioned the usefulness of fossils in a systematic study of scombroids, since gill arch characters cannot be well recorded from fossil taxa. I have realised the importance of the synapomorphies of certain groups based on gill arch characters and have employed the characters of Johnson (1986) which seem the most relevant. I do not regard the amount of missing gill arch-data of fossil taxa as a problem, because there are many anatomical and osteological characters of scombroids remaining to lay a sound basis for phylogenetic research. A choice of gill arch character that fossilise less badly than others could not be made. Hence, I made the choice to include those gill characters that seem to convey the strongest phylogenetic signals according to Johnson (1986), such as those that are indicated as synapomorphies of scombroids or the *Acanthocybium*-billfish clade (see Johnson, 1986).

Some of the characters of the recent papers had to be revised, such as characters 18 and 18' of Johnson (1986) (see my description of soft-tissue characters). Some characters I have used consist of a combination of what was before described as more than one separate character, such as the fusion pattern of

the caudal complex bones of gempylids in Collette *et al.* (1984). Some characters used in my data matrix have appeared as a result of my own observation of scombroid material, and have not been mentioned before as a synapomorphy within scombroids. An example is the relative size of the lachrymal bone.

Some of the characters have been formulated after observation of the fossil material, in which characters, character states or character combinations are seen which are not present in the Recent taxa or were not included in a phylogenetic analysis. Maybe these characters were not included because the variability of the character in question can be observed only after also having seen the fossils, or maybe for other reasons unknown to me. Examples of these characters are the shape of the anterior margin of the vomer and the number of tooth rows in jaws.

Some of the characters that I recorded from the literature have come from sources in which specific groups of scombroids or outgroups are described. For the outgroup taxa, there are Suda (1996) for *Trachurus*, Tyler *et al.*, (1989) and Gregory & Conrad (1943) for *Luvarus* (louvar); Bond & Uyeno (1981), Potthoff *et al.* (1980) and Roule (1922) for *Scombrolabrax*. For scombroids, these references are: Schultz (1987), Conrad (1937), Gregory & Conrad (1937), Nakamura (1968, 1985) and Davie (1990) for billfishes; Russo (1983) and Matsubara, & Iwai (1958) for gempylids; Parin & Astakhov (1987) and Parin (1990) for *Rexichthys*, Tucker (1956), Parin & Bekker (1972) and Gago (1997, 1998) for trichiurids; Kohno (1984) for *Gasterochisma*, Collette (1978) for scombrids in general, Matsui (1967) for *Scomber* and *Rastrelliger*; Collette & Russo (1984) for Scomberomorini; Collette & Chao (1975) for Sardini; Nakamura (1965), Collette & Nauen (1983) for Thunnini, and Nakamura & Mori (1966) and Graham & Dickson (2000) for *Allothunnus*. In the series "Introduction to Scombriform fishes", I. Nakamura extensively describes and discusses functional morphology of scombroids from an evolutionary point of view. This series contained a large number of useful references for character description and understanding: Nakamura (1989b, 1990, 1991a,-d, 1992, 1993a, d, e, 1994a, b). Information on the distribution of red muscle in mytomes came from Sharp & Pirages (1978) and Brill (1996). While choosing these characters, my choice was based on criteria like: Does the character display a variety of states which seems to characterise certain (sub)groups? Does this character clearly identify the different taxa? I have tried to make a concise data matrix, aiming to include characters that mostly seem to express synapomorphies and as few autapomorphies as possible.

Not all scombroid and outgroup taxa could be studied from original material and some taxa were not represented by adequate specimens, which means that not all character (-states) could be recorded at first hand. The character-data used for phylogenetic analysis taken from the literature, but without being accompanied by

my own observations, are indicated as such, within the text of this chapter and the data matrix (Appendix 4).

Below follows a detailed description of the various characters of scombroids. These are divided into skeletal, soft-tissue and larval-development characters. The character codings, as adopted in the data matrix are indicated with the descriptions below. The position of a character under a higher- or lower-ranked caption below does not imply anything concerning the weight of the character; it is simply the way in which the characters are described. Some of the characters employed here are used before, either exactly as mentioned in this chapter, in another form, or in part. Sometimes a character of my phylogenetic analysis is part, or an amalgamation of, a previously used character or characters. In such cases, the original description of the character is referred to. The characters in question come from phylogenetic analyses by Russo (1983, gempylids), Collette *et al.* (1984, scombroids), Collette & Russo (1984, Scomberomorini), Johnson (1986) and Gago (1997, 1998, trichiurids). The analyses of Carpenter *et al.* (1995) are not new phylogenetic analyses as such, but evaluations of Johnson's (1986) earlier analysis, in which some of Johnson's original characters or datamatrix entries have been modified. It is worth mentioning here that two of the authors of these evaluations, Collette and Russo, are contributors to the first phylogenetic analysis of scombroids (Collette *et al.*, 1984). Graham & Dickson (2000) conducted a phylogenetic analysis to test the hypothesis that *Allothunnus* belongs to the Thunnini. They do not provide a matrix with character numbers, but indicate that their analysis is based on the datamatrix of Carpenter *et al.* (1995) with the addition of two characters of their own, which they describe.

5.2 SKELETAL CHARACTERS

The skeletal characters can be subdivided into characters of the skull, the vertebral column, the paired and unpaired fins and the caudal region. The osteological terminology used here is drawn mostly from De Sylva (1955). Although different terminology is mostly used for descriptive osteology, this terminology is often maintained for scombroids.

5.2.1 Skull.

The skull can be divided into the braincase (which is what De Sylva, 1955 calls neurocranium) and the branchiocranium (appendages to the neurocranium). A special section is reserved for the rostrum of billfishes.

5.2.1.1 Braincase.

The neurocranium is a fairly compact entity with varying shapes (Fig. 5.1). Several of the components of this construction of different bones serve as phylogenetically significant characters, as is outlined below.

Frontal. Most of the dorsal surface of the braincase is occupied by the frontals: a pair of more or less elongated, bones, with more or less pointed apices (Fig. 5.2a-g). In *Eocoelopoma*, a species formerly known as *Eocoelopoma hopwoodi* (see § 7.3) and *Palaeothunnus*, the anterior part of the frontal, just anterior of the three pairs of dorsal cranial grooves, is thickened and ornamented with fine lines (Fig. 5.2b). This character, however, is considered in assessing phylogenetic relationships. There are other characters that identify the taxa in question.

Supraoccipital. The most posteriorly situated (single) bone in the neurocranium is the supraoccipital. It forms a crest that extends a short way posteriorly (Fig. 5.1). The variety of shapes and sizes of this element, difficult to quantify, have not been used in the phylogenetic analysis.

Cranial crest. In the plesiomorphous condition there is no cranial crest **(character 6, state 0)**. In the Scomberomorini, Sardini and Thunnini, and in the trichiurid *Assurger* there is a low cranial crest, not deeper than the cranium below it **(state 2)**. The crest consists posteriorly of an enlarged supraoccipital crest and anteriorly of dorsal outgrowths of the frontals, extending to the anterior tip of the frontal (Fig. 5.1). In the outgroup taxon *Coryphaena*, as well as in *Gasterochisma* and the trichiurids *Evoxymetopon* and *Tentoriceps*, the crest is almost as deep as, to deeper than the underlying neurocranium (Fig. 5.1c) **(state 3)**. The trichiurids *Trichiurus*, *Lepturacanthus*, *Lepidopus* and *Euplorogrammus* have shorter, small crests, which are not extended rostrally to the rostral apex of the frontals (Fig. 5.1d) **(state 1)**. The often confused trichiurids *Lepidopus* and †*Anenchelum* differ by the presence of a cranial crest in *Lepidopus* and its absence in *Anenchelum*. The size of the supraoccipital crest is character 20 in Russo (1983).

Parietal. The parietals are paired. Both parietals flank the supraoccipital (Fig. 5.2a). I have observed no variety in the parietals that I could quantify for use in the phylogenetic analysis.

Postero-superior fossa This is a pit in the postero-lateral part of the frontal, which serves for muscle attachments. This fossa is, other than here, only thus named by Casier (1966). In most scombroids, the postero-superior fossa is clearly situated posterior to the midline of the orbit (Fig. 5.2d) **(character 3, state 0)**. In †*Eocoelopoma*, this fossa is situated near the middle of the orbit (Fig. 5.2b) **(state**

1). In *Woodwardella* (Fig. 5.2c), these fossae are situated almost at the anterior margin of the orbit (**state 2**).

Supratemporal groove. The dorsal surface of the skull contains at most three broad pairs of grooves, which cover areas formed by different components of the braincase. Of these three, the supratemporal groove (*cf.* Allis, 1903) is the most medially situated. This groove is formed by depressions and/or inclinations of the parietal, the supraoccipital and the frontal. This groove can be long: extending towards the anterior tip of the frontal (Fig. 5.2a), in Scomberomorini, Sardini, Thunnini and †*Eothynnus* (**character 2, state 1**), short: anteriorly bordered by a frontal crest (Fig. 5.2d), in most scombroids (**state 0**), or absent (**state 2**) in *Gasterochisma* (Fig. 5.2e), the istiophorids and *Luvarus*.

Frontoparietal fenestra. (Figs. 5.2a, g). In the Thunnini except *Allothunnus* and *Auxis* there is a pair of large foramina, at the junction of the frontal, the parietal and the supraoccipital (**character 4, state 1**). In other groups, these foramina are absent (**state 0**). This is also character 24 of Collette *et al.* (1984). A function of these foramina is unknown, but Collette (1978) suggested that these could, covered by connective tissue, serve as pressure valves. The brain, in a tightly enclosed box, is warmer than the surrounding water. The pressure within this structure might increase to such a degree that it can damage brain tissues if it was not for these pressure valves. Nakamura (1994a) thinks that the degree of pressure on the connective tissue on these fenestra is transferred to the semicircular canals of the ear. Thus, these foramina function as depth-detectors. Thunnini are known as epipelagic fishes, but are also known to dive into deeper, cooler water while hunting, hereby aided by their high body temperature (see also Chapter 4). Yet another suggestion comes from Graham & Dickson (2000), who suggest that the frontoparietal fenestra are thermal windows for heat conduction into the brain and retina. It might be that these parietal foramina have evolved to serve various functions.

Pineal window. *Acanthocybium*, *Grammatorcynus*, the Sardini and Thunnini possess a clearly discernible foramen at the midline of the skull, just rostral to the junction of the frontals with the supraoccipital (Fig. 5.2a, f, g) (**character 5, state 1**). This pineal window is, generally speaking, largest in Thunnini and smallest in *Grammatorcynus* (Fig. 5.2f). Some gempylids also possess a narrow slit between the frontals, uncovering the pineal organ. In some specimens of Sardini the margins of the pineal window undulate, narrowing or (almost) closing the window in some sections. In other scombrids, this window is missing or present by only a small inconspicuous slit (**state 0**). In Collette & Russo (1984, character 12) this is a three-state character: present, reduced and absent. The pineal window (partially)

uncovers the region of the central nervous system called the pineal organ. Research by Murphy (1971) indicates that the pineal sensory cells are structured like retinal photoreceptor cells. This seems to support Rivas (1953) hypothesis that the pineal window is used as a photoreceptor in migratory behaviour. Rivas (1953) and Nakamura (1994a) noticed that sunlight can pass through the window to the pituitary organ in the brain. This might stimulate seasonal or monthly rhythms in the life cycles of these fishes. This agrees with earlier suggestions that the pineal window has a role in migratory behaviour. Murphy (1971) also found that the pineal window and its covering and underlying tissues are capable of light transmission. More recently, Ekström & Meissl (1997) found that the pineal organ is indeed a photosensory organ. Based on their experiments, they hypothesise that pineal organ is part of the system that is responsible for correct timing of physiological rhythms. The exact role of the pineal organ within that system is not yet known, and the role of the organ in scombrids specifically has not been researched. Whatever it might be, it seems likely to me that a foramen in the skull, uncovering the pineal organ, enhances its efficiency. The larger the foramen is, the more impulses the pineal organ receives.

Nasal. There is a pair of nasals. They are usually small, long and slender bones, inserted near the apex of the frontal (Fig. 5.2a, f). Some confusion exists regarding the nasal of *Xiphias* and the istiophorids (see description of the billfish rostrum). I have not been able to quantify the variability of the nasals for phylogenetic analysis.

Pterotic. The pterotic is the most lateral bone in the skull and is also extended posteriorly considerably. In most scombroids the pterotic is a short winged structure (Fig. 5.2a, d, e, f) (**character 8, state 0**), but in the tuna genera *Auxis*, *Euthynnus* and *Katsuwonus* the pterotic ends in a long spine (Fig. 5.2g) (**state 1**). My state 0 here shows a variability which is expressed by states 0 and 1 in Collette & Russo's (1984) character 15. Judging by its shape and position on the skull, the primary function of the pterotic is for muscle insertion.

Intercalar. The intercalar is the most posterior bone in of the dorsal surface of the braincase. In the plesiomorphous condition, the margin of the intercalar is straight or nearly so (**character 10, state 0**). In some taxa, however, the margin is slightly undulated, so a short caudal projection is formed (Fig. 5.2a, g), in some gempylids, the fossil *Sphyraenodus* and some *Scomberomorus* (**state 1**). In other taxa, this caudal projection is more pronounced and longer (**state 2**): in some *Scomberomorus* and in all *Auxis, Euthynnus* and *Katsuwonus* (Nakamura, 1965). The size of the intercalar protuberance is character 17 in Collette & Russo (1984).

This protuberance functions as an articulation point for the posttemporal, which connects the shoulder girdle to the skull.

Epiotic The paired epiotics border on both the parietal and the supraoccipital. The epiotic is a pointed bone with its apex pointing posteriorly. This is normally a simple blunt apex (Fig. 5.3a) (**character 9, state 0**). In the Thunnini, the apex is slightly bifurcated into two short, blunt apices (Fig. 5.3b). In istiophorids and some gempylids the apex is flattened and extended further posteriorly (Fig. 5.3c). In *Sphyraena* and the mugilids the apex is long and frayed (Fig. 5.3d) (**state 1**). The function of the epiotic seems primarily for articulation of the head with the shoulder girdle.

Ethmoid. The ethmoid is a median, single bone, covered dorsally by the frontals and flanked ventrally by the vomer (see below). The ethmoid normally has an anterior blunt ending (**character 7, state 0**). In the Scomberomorini except *Grammatorcynus* (see Collette & Russo, 1984), mugilids, †*Scombramphodon*, †*Sphyraenodus* and a taxon formerly known as *Scombrinus macropomus* (Agassiz, 1844) the ethmoid has an emarginated anterior margin, creating an almost fork-shaped structure (Fig. 5.4b) (**state 1**).

Vomer. The vomer is the most anterior bone of the ventral side of the neurocranium (Fig. 5.5a-e). It is an elongated bone that is posteriorly inserted into the parasphenoid (see below). Together with the parasphenoid, it forms the supporting axis of the roof of the mouth. The vomer normally has a blunt anterior edge (**character 14, state 0**), which, in the plesiomorphous condition contains a few conical teeth (Fig. 5.5c) (**character 13, state 0**). In the Sardini, Thunnini and Scomberomorini, instead, there is a patch of villiform teeth (Fig. 5.5b, e). The presence or absence of vomerine teeth is used as a phylogenetic character in Russo's (1983, character 11) analysis of gempylids. In *Scomberomorus* and *Acanthocybium*, the anterior margin of the vomer forms a rostrad-pointing spatula-like plate (**character 14, state 1**). In *Scomberomorus* this plate protrudes far beyond the anterior end of the skull roof. In *Acanthocybium* and *Grammatorcynus* (see Collette & Russo, 1984) this is less pronounced. This is character 31 in Collette & Russo (1984). Vomerine teeth are missing (**character 13, state 1**) in the outgroup taxa *Valamugil*, *Liza* and *Mugil*, the trichiurids, the gempylids *Diplospinus*, *Epinnula*, *Gempylus*, *Nealotus*, *Nesiarchus*, *Paradiplospinus*, *Dicrotus* and *Thyrsitoides*, the billfishes, *Rastrelliger*, *Sarda* and *Euthynnus alletteratus* (Rafinesque-Schmaltz, 1810). Russo (1983, character 13) mentions three character states in the anterior extent of the vomer. However, there is a sharp boundary between these character states, and indeed the anterior extent of the

vomer in most scombroids, compared to the state in the Scomberomorini. Hence, all three character states of Russo's character 13 can be incorporated in my character 14.

Parasphenoid. Together with the vomer, the parasphenoid forms the axis of the roof of the mouth (Figs. 5.1 and 5.5). Anteriorly, it extends with a double fork-shaped apex, in between which the vomer is inserted. Posteriorly, it reaches the end of the neurocranium. No characters of the parasphenoid have been considered in the phylogenetic analysis.

Lateral ethmoid. The lateral ethmoids are paired and are situated just posterior to the ethmoid and dorsal of the vomer (Fig. 5.5a). The lateral ethmoid does not seem to display a variability that can be quantified and coded for the phylogenetic analysis.

Infraorbitals (lachrymal). Infraorbitals are a series of mostly small, thin bones, which form a circular arch around the orbit of the neurocranium (Fig. 5.6). The most ventral element of this infraorbital series, infraorbital 1, is much larger than the others and is more widely known as the lachrymal. I have observed that the relative size of the lachrymal is different in various taxa. In *Sphyraena*, trichiurids, most gempylids, in Scombrini, Scomberomorini, *Sarda*, *Blochius*, *Eocoelopoma* and a new fossil taxon (see § 7.3), the lachrymal is longer than the maximum diameter of the orbit (Fig. 5.6a) (**character 1, state 1**). In other taxa considered, the lachrymal is shorter (Fig. 5.6b) (**state 0**).

Alisphenoid, basisphenoid and sphenotic. These are bone elements which are mostly or completely situated at the ventral side of the skull, concentrated around a large optic foramen which opens into the brain chamber (Figs. 5.1, 5.5d). I have not seen a variability that could be quantified or coded for the phylogenetic analysis in any of these bones. The foramen is flanked on the left and the right by a pair of alisphenoids (often called pterosphenoid). Posteriorly, the foramen is bordered by a Y-shaped basisphenoid, which extends ventrally to abut with the parasphenoid. The alisphenoid is flanked by a pair of sphenotics, which are also visible on the dorsal side of the skull and abut with the pterotics posteriorly.

Prootic. The prootics are paired and lie posterior to the alisphenoid and the basisphenoid. They are laterally flanked by the sphenotics and the pterotics and are abutted ventrally by the parasphenoid (Fig. 5.5a, b, d, e). In the Thunnini, the prootic develops oblique, broad outgrowths (Figs. 5.5a, e). In *Auxis*, *Euthynnus* and *Katsuwonus*, this outgrowth partially covers a deep depression in the prootic (Fig.

5.5a). This outgrowth has presumably evolved to enhance muscle attachments. Characters of the prootics have not been considered in the phylogenetic analysis.

Exoccipital. Exoccipitals are paired bones, close to the axis of the skull, laterally flanked by the intercalars, which are also visible in dorsal aspect of the braincase (Figs. 5.2 and 5.5). I have not seen a variability in the exoccipitals that could be quantified and coded for the phylogenetic analysis.

Basioccipital. The basioccipital is situated postero-median in the neurocranium, flanked by the exoccipitals (Fig. 5.5d). It does not display a variability that can be used in the phylogenetic analysis.

5.2.1.2 Branchiocranium.

The branchiocranium is formed by the "appendages to the braincase": the jaws, palatine arch, the hyoid arch, the glossohyal, urohyal, the opercular bones and the branchial apparatus.

Maxilla. The maxilla is the part of the upper jaw that articulates directly with the braincase (to the vomer). It is a slender, edentulous bone, with a spatula-like posterior apex that is connected to he lower jaw (Fig. 5.7a, b) by ligaments. I have not seen a variability in the maxilla that could be quantified and coded for the phylogenetic analysis.

Supramaxilla. In most of the considered ingroup taxa, *Sphyraena* and outgroup taxa like *Scombrolabrax* possess a small bone, the supramaxilla (**character 11, state 0**), which covers the distal spatula-like end of the maxilla (Fig. 5.7a). The outgroup taxa *Trachurus* and *Luvarus* and the billfishes lack this supramaxilla (**state 1**).

Premaxilla. The premaxilla is the anteriormost element of the upper jaw. In most teleosts and also most outgroups of scombroids, the premaxilla and maxilla articulate at their distal apices (Fig. 5.8) (**character 12, state 0**). In scombroids, *Luvarus*, *Sphyraena* and *Scombrolabrax* the maxilla also neatly locks with a rostral process into the premaxilla, to create a tightly bound upper jaw complex (Fig. 5.7a) (**state 1**). This is character 19 of Collette *et al.* (1984) and character 9 of Johnson (1986). This is an adaptation to biting chunks off large prey, rather than sucking in small prey, which many other fish with a protractile mouth do (Fig. 5.8). The premaxilla develops an ascending process anteriorly, which is bifurcated distally into two blunt apices (Fig. 5.9). The axial apex is normally the most pronounced (Fig. 5.9c), which is clearest in a taxon formerly known as

Scombrinus macropomus (see § 7.3), *Scombramphodon* and *Sphyraenodus*. In Scomberomorini, except *Grammatorcynus*, the two processes seem to be fused and cannot be distinguished (compare Figs. 5.9b). Most of the premaxilla consists of the posterior straight shank. In the Scomberomorini, a species formerly known as *Scombrinus macropomus* and *Scombramphodon* the ascending process is larger and makes a more acute angle with the posterior shank. In *Scomberomorus*, the ascending process of the premaxilla takes up 31-48 % of the total premaxilla length and makes an angle of 32°-61° with the shank (Collette & Russo 1984). These premaxilla characters concerning the relative size of the premaxilla are not always easy to measure in damaged fossils and there are other characters to identify the taxa in question.

Dentary. The dentary is the principal bone of the lower jaw. Posteriorly, the dentary is bifurcated (Figs. 5.7, 5.10). The split between the two posterior apices lies rather deep anteriorly. The dentary is tapered rostrad. Most scombroids have a dentary with a small, inconspicuous anteroventral projection ("chin"). In a few scombroids, this chin deserves further comment. In Sardini (Fig. 5.10a) and Scomberomorini (Fig. 5.10b), except *Acanthocybium* (Fig. 5.10c), the chin is projected straight ventrad, and this ventral projection is followed by an emargination. In *Sarda*, this emargination is deepest. In the Thunnini and *Acanthocybium* the chin is oblique, projects anteroventrad and is not followed by an emargination. It thus looks as if the dentary has two blunt anterior apices. The lower jaw is normally shorter than the upper jaw (**character 19, state 0 and 1**, see also § 5.2.1.3). In trichiurids and gempylids, the dentary protrudes the upper jaw anteriorly (**state 2**).

Predentary. In istiophorids, the dentary is preceded by a small triangular toothed predentary bone (Fig. 5.10d). This structure is a neomorph (Fierstine & Applegate, 1968), not found in any closely related fish taxon. Istiophorids can, however, be diagnosed with more obvious characters than the presence of the predentary. Hence, this character has not been adopted in the phylogenetic study.

Angular. The angular (*cf.* Collette & Chao, 1975; Collette & Russo, 1984) is the bone which indirectly articulates the lower jaw to the braincase and the upper jaw to the lower jaw (Fig. 5.7). A large triangular anterior process (often called articular, Fig. 5.11a) fits into the dentary. A dorsal and a ventral process (Fig. 5.11b) grip onto the dorsal and the ventral posterior process of the dentary respectively (except in *Scomber* and *Rastrelliger*, see Fig. 5.11c). Postero-ventrally, the angular has a facet for articulation with the quadrate, the bone which indirectly (through the hyomandibular, see below) connects the lower jaw to the neurocranium. Postero-

dorsally, the angular articulates with the posterior apex of the upper jaw. Characters of the angular have not been adopted in the phylogenetic study.

Retroarticular. The retroarticular is a rhomboid bone (often called angular), attached to the posteroventral margin of the angular (Fig. 5.11a). I have not discovered a variability in retroarticulars to quantify or code for the phylogenetic analysis.

Dentition. Most of the studied fishes have a single row of teeth in sockets (**character 20, state 0**). In billfishes and *Coryphaena*, these teeth are present in multiple rows (**state 3**) (Fig. 5.12a). Billfish teeth are almost villiform. The presence of multiple rows of minute teeth in billfishes is character 57 in Johnson (1986). The teeth of billfish are minute cones, and in that respect do not differ from the conical teeth of most other groups (**character 22, state 0**). Schultz (1987) separated a new family Tetrapturidae from within the istiophorids with the diagnostic feature of having a median edentulous zone in the tooth patch of the rostrum. However, my observations have not supported this division. Also, Fierstine & Voigt (1996) have shown that Schultz (1987) misinterpreted the infraspecific variation in these taxa. In *Xiphias*, these teeth disappear in ontogeny, so the adults are toothless (**state 4**). The specimens of the fossil billfish *Blochius* (see chapter of Systematic Palaeontology) that I have seen have no teeth preserved. However, Schultz (1987) mentioned two juvenile specimens in the Natural History Museum in Vienna which have numerous denticles. A photograph of specimen S40 of the Museo Civico di Storia Naturale, sent to me by H.L. Fierstine, seems to show small teeth as well. However, it is not certain that this specimen is indeed a *Blochius* (Fierstine, pers. comm., 1999). *Scombramphodon* and a species formerly known as *Cybium dumonti* Storms, 1895 (see § 7.3) have two complete tooth rows (**state 2**). *Wetherellus* and the species formerly known as *Scombrinus macropomus* have a complete inner tooth row and an incomplete outer one (**state 1**), with smaller teeth (Fig. 5.12b, c), in both the upper and lower jaw. The preservation of the fossil specimens was such, that the incompleteness of the outer tooth row can be certified. In the anterior part of the jaw bones the outer tooth row stops and only the inner tooth row is still present. Besides the serial teeth, the gempylids and the trichiurids have one or more pairs of large fangs in the premaxilla and the anterior tip of the dentary (**character 21, state 1**). These fangs are significantly larger than the serial teeth (Figs. 5.7, 5.9, 5.12d). *Sphyraena* has one fang anteriorly in the dentary and †*Abadzekhia* has one fang anteriorly in the premaxilla. Other groups lack these fangs (**state 0**). These fangs are the inner row of premaxillary teeth in character 18 of Collette *et al.* (1984). See also character 32 of Johnson (1986). In most of the studied groups, teeth are conical or slightly

compressed as in gempylids and trichiurids (**character 22, state 0**). Using Nakamura (1991c)'s terminology, the somewhat flattened teeth as in gempylids and trichiurids are teeth of the canine type. In gempylids the teeth tend to be retrorse (compare Figs. 5.7, 5.9 and 5.11a) (**character 23, state 1**). In other groups, the teeth are straight (**character 23, state 0**). In some trichiurids, the teeth are barbed (Fig. 5.7) and some larger teeth are curved into an S-shape (Fig. 5.12e). The teeth of Scomberomorini are also somewhat compressed laterally. In *Grammatorcynus*, these teeth are sharpest and they are slightly blunter in *Scomberomorus* (Fig. 5.12f). In †*Scomberodon* and a species formerly known as †*Cybium dumonti* and an as yet undescribed fossil scombermorin (see § 7.30 the teeth are not only laterally compressed, but also very tightly packed and are blunt-tipped with an almost rounded apex, rather than sharp (**character 22, state 1**). In *Acanthocybium* (Fig. 5.9) the teeth are similar but also have and a serrated cutting edge (**character 22, state 2**). The serrations are only visible through the microscope, so cannnot be seen in Fig. 5.9b. Sardini and can be distinguished from Thunnini by the fact that Sardini have large, rounded conical teeth and Thunnini have much smaller, inconspicuous teeth.

Palatine arch. The palatine arch, forming of the roof of the mouth, is formed by a series of lateral bones: the palatine, pterygoid bones, quadrate and symplectic.

Palatine. The palatine is a small, thin bone, articulated with the vomer through a narrow anterior process. Its posterior end, mostly lamellar in a horizontal plane, is connected to the endopterygoid and the ectopterygoid (Fig. 5.13a). The palatine normally has one or more rows of small conical or villiform teeth (Fig. 5.13a, b) (**character 15, state 0**). Billfishes, *Auxis* and *Rastrelliger* have edentulous palatines (**state 1**). This character is also used in a phylogenetic analysis of trichiurids (Gago, 1998).

Pterygoid bones (Fig. 5.13a). The ectopterygoid is a T-shaped bone with the crossbar lying vertical, and is connected to the palatine by its horizontal process. Dorso-median to the ectopterygoid and the posterior end of the palatine is the endopterygoid: a thin, lamellar bone, mostly ovoid in shape. Postero-ventrally, the ectopterygoid connects to the quadrate. Postero-dorsally, the ectopterygoid is partially covered by the metapterygoid, which abuts the quadrate ventrally. The variety of the characters of the pterygoid bones is not obviously visible, so no pterygoid bone characters are included in the phylogenetic analysis.

Quadrate and symplectic. The quadrate is a triangular bone that connects the palatine arch and the lower jaw to the neurocranium through the hyoid arch (see below). The apex of the triangle is an articular process that articulates with the angular. The anterior margin of the quadrate is covered by the ectopterygoid. Dorsally, the quadrate abuts with the metapterygoid. Postero-ventrally, the quadrate

develops into a process, which creates a groove into which the small, thin symplectic fits (Fig. 5.13a, c). The variability of characters in the quadrate and the symplectic is difficult to quantify and code for the phylogenetic analyses, hence no characters of these are included in the data matrix.

Hyoid arch. The hyoid arch is a chain of bones that connects the palatine arch, the lower jaw, the opercular series and the branchial arch to the neurocranium. It consists of the hyomandibular, the hyoid complex, the basihyal and the urohyal (Figs. 5.13a, c, 5.14a-c).

Hyomandibular. The hyomandibular abuts ventrally with the quadrate, together with the metapterygoid, which also partially covers the hyomandibular on both its left and right sides (Fig. 5.13a). The hyomandibular articulates with the braincase by fitting in sockets formed by the pterotic and sphenotic. It also contains a postero-dorsal articular facet, on to which the operculum articulates (Figs. 5.7 and 5.13a) No characters of the hyomandibular are used in the phylogenetic analysis, since I could not discover codeable characters for the data matrix.

Hyoid complex. Most of the hyoid complex, which connects the branchial apparatus to the hyoid arch, consists of paired bones. The basihyal and the urohyal are unpaired. The paired bones are the hypohyal, ceratohyal, interhyal, and a series of seven branchiostegal rays (Fig. 5.14b-d).

Basihyal (also called glossohyal, for example Collette & Russo, 1983; Gago, 1998; Nakamura, 1991d). The basihyal is the anterodorsally situated singular bone of the hyoid complex, which supports the tongue. It is flanked on both sides by the arches of the hyoid complex (Fig. 5.14a). The basihyal in gempylids (except *Lepidocybium*) and trichiurids has a distinct ventral keel and is slender and elongated. In other taxa it is short and spatulate, without a ventral keel (compare Figs. 5.14 and 5.15a). The gempylids and the Sardini *Cybiosarda* and *Orcynopsis* have two small tooth patches on the dorsal surface. These are larger in *Cybiosarda* (Figs. 5.15b, c). *Gymnosarda* has similar tooth patches, about the same size as in *Orcynopsis*, but these are attached to the fleshy part of the tongue rather than the basihyal. LaMonte (1958) has noted the presence of small denticles on the tongue of *Makaira*. Characters of the basihyal are not adopted in the phylogenetic analysis. There are other characters to identify the taxa in question, and the basihyal characters do not fossilise well.

Urohyal. The urohyal is an upaired, long and thin bone, placed anteroventrally between the paired arches of the hyoid complex. From its insertion it is directed posteriorly (Fig. 5.14a). Its shape varies greatly within the scombroids: in Thunnini, it has a thickened ventral margin (Fig. 5.16a); in Scomberomorini and istiophorid it has a thickened dorsal margin, which is posteriorly bifurcated; and in

istiophorids there are also two postero-ventral spines (Fig. 5.16b). These characters, however, do not fossilise well and there are other characters that identify the taxa in question. Hence, the urohyal characters are not used in the phylogenetic analysis.

Hypohyals. Each of the paired hyoid complexes has a pair of basal hypohyals (Fig. 5.14). In Sardini and Thunnini, the suture between the hypohyals is not clearly visible. The strongly similar *Scomber* and *Rastrelliger* differ by the fact that the hypohyals in *Scomber* are much longer The characters of the hypohyals have not been employed in the phylogenetic study.

Ceratohyal. Posteriorly, the hypohyals are followed by a single ceratohyal, which generally is the largest component of the hyoid complex. The ceratohyal is widened posteriorly. The ventral margin of the ceratohyal is normally straight and smooth or just slightly undulated (**character 25, state 0**), but in Thunnini, *Sphyraenodus*, *Scomberomorus* and some species of *Sarda*, it has small ventral projections (**state 1**), where the branchiostegal rays articulate with the ceratohyal (Fig. 5.14d). The ceratohyal also contains a longitudinal ceratohyal groove (not clearly visible in Sardini and Thunnini), in which there might be a ceratohyal window (Fig. 5.14b) (**character 26, state 1**). This is observed in the outgroup taxon *Trachurus*, in *Sphyraena*, most trichiurids, the gempylids *Diplospinus*, *Nesiarchus*, *Lepidocybium*, *Nealotus*, *Neoepinnula*, *Nesiarchus* and *Thyrsites*. Russo (1983) noted that the window was absent in adults of *Diplospinus* and *Nesiarchus*. This window is also present in the trichiurids *Aphanopus*, *Benthodesmus*, *Eupleuogrammus*, *Evoxymepoton*, *Lepturacanthus* and *Tentoriceps*. The window may be present or absent in *Scomberomorus*, and is present in *Acanthocybium*, *Grammatorcynus*, some specimens of *Scomber* (Fig. 5.14b), in *Gasterochisma* and Sardini. Other groups lack this window (**state 0**).

Epihyal. The epihyal is attached posteriorly to the ceratohyal through a median series of odontoid processes in both epihyal and ceratohyal, while at the dorsal and ventral ends, the epihyal and ceratohyal are adjoined by cartilage. The epihyal has a semi-ovoid outline, with a narrowed caudal apex, which fits into a socket on the axial surface of the interoperculum. The epihyal is a relatively short bone, except in *Rastrelliger*, where it is about as long as the ceratohyal (Figs. 5.14b, c). This character has not been used in the phylogenetic analysis. This character seems to be only relevant in the identification between *Scomber* and *Rastrelliger*.

Interhyal. The interhyal is a small rod which connects the epihyal to the hyomandibular, through the posterior apex of the epihyal. It is also connected to the internal surface of the interoperculum by cartilage (Fig. 5.14d). I have found no quantifiable and codeable characters for the phylogenetic analysis in the interhyal.

Branchiostegal rays. On each of the paired arches of the hyoid complex, there are seven rib-like bones, the branchiostegal rays. These serve as support for the

membrane that covers the gill cavity ventrally. There are four attached to the ventral margin of the ceratohyal. Normally, there are three rays attached to the epihyal, but sometimes the fifth is attached at the symphysis of the ceratohyal with the epihyal, as in *Scomber* (Fig. 5.14b); or to the ceratohyal, as in *Istiophorus*. Often, the last branchiostegal ray is slightly enlarged, but not significantly larger than the preceding rays (**character 27, state 0**), except in the studied mugilids and *Rastrelliger* (Fig. 5.14c) (**state 1**), where it is flattened into a large plate.

Opercular series. The opercular bones form the freely movable gill cover. The series consists of the operculum, preoperculum, subopercular and interopercular (Fig. 5.17).

Operculum. The operculum is a thin bone with a variety of ovoid- or rhomboid-like shapes but always anteriorly tapered into an articular socket which fits on to a posterodorsal facet of the hyomandibular. The outgroup *Trachurus*, the mackerels *Scomber* and *Rastrelliger*, gempylids and trichiurids have a posterodorsal notch in the operculum (**character 35, state 1**), which other groups appear to be missing (**state 0**). Only in a fossil trichiurid from the Isle of Mors, Denmark (see § 7.3) does the operculum not seem to be thus emarginated. The outgroup taxa *Trachurus* and *Scombrolabrax*, gempylids, *Scomber* and *Rastrelliger* have deepened opercula, with a sharp and acute ventral angle (Fig. 5.18a). In gempylids and trichiurids, the operculum is quadrilateral. In the trichiurids, the posterior and ventral margins of the operculum are splintered or fimbriated (Fig. 5.18b) (**character 36, state 1**). In other groups these ventral margins are smooth (**state 0**), although they can appear to be splintered in large specimens, after preparation of the skeleton. In these cases, smaller specimens of the same taxon never have fimbriated opercula (as in *Xiphias*), but all post-larval specimens of trichiurids have opercular bones with splintered margins. Fimbriations of margins of opercular bones are also described in Johnson (1986, character 26) and Gago (1998, characters 1,3).

Preoperculum. The preoperculum is situated anteroventral to the operculum. It locks neatly onto the hyomandibular by a thickened inner surface and ventrally supports the quadrate (Fig. 5.19a). At the outer margin, the preoperculum has openings to pores that originate at the anteromedian margin. These are the pores of the branched preopercular sensory canal. Typically, the preoperculum is crescent-shaped. In gempylids and trichiurids, the preoperculum is dorsally wide, tapering ventrad. In the Scomberomorini, the preoperculum is somewhat irregular in shape (Fig. 5.19b). In *Scomber*, *Rastrelliger* and Sardini, it is deep-crescent shaped (Fig. 5.19c) and in Thunnini it is mostly shallow-crescent shaped, being the longest at the corner of the two "crescent arms". This condition is most pronounced in the

Thunnini *Auxis, Euthynnus and Katsuwonus* (Fig. 5.19d). No characters of the preoperculum have been used in the phylogenetic analysis.

Subopercular. The subopercular is a triangular thin bone with an acute dorsal angle. It has an anteroventral pointed projection that points dorsad. The operculum is locked into the corner that is created by this corner. The subopercular is deepest and most slender in *Rastrelliger* and *Scomber* (Fig. 5.20a). In the trichiurids only, the ventral margin of the subopercular is splintered or fimbriated (**character 36, state 1**); in other groups it is not (**state 0**). Its ventral free margin is normally convex (Fig. 5.20b) (**character 37, state 0**), but in the genera *Trichiurus*, *Lepturacanthus* and a new genus and species described in § 7.3, this margin is concave (Fig. 5.20c) (**state 1**).

Interoperculum. The interoperculum is the most anteroventrally situated opercular bone and is partially overlapped, or at least bordered by, every other opercular bone (Fig. 5.17). It has roughly a triangular shape, with the apex pointing anteriorly. It contains no phylogenetically useful characters.

Branchial arches (Fig. 5.21). The branchial arches consist of five pairs of gill arches. The elements of the arches are the basibranchial, hypobranchial, ceratobranchial, epibranchial and pharyngobranchial (Fig. 5.21a). These elements are to different degrees covered by splint-or plate-like gill rakers and tooth patches (Fig. 5.21b-d). The non-bony gill filaments, the structures that support the gas exchange surface, are ventrally attached to the branchial arch (Fig. 5.21b). Except for characters of the pharyngobranchials and their articulation with epibranchials, no other characters of the branchial arch are employed in the phylogenetic analysis. I have mentioned before (§ 5.1) why I have limited the use of branchial arch characters in the analysis.

Basibranchial. There are three basibranchials, which lie horizontally in the midline of the fish. These are three rod-like bones that form the ventral basis from which the rest of the branchial arch springs (Fig. 5.21a). The anteriormost basibranchial is covered by the basihyal.

Hypobranchial. The first three branchial arches have hypobranchials that are connected to the basibranchials. The first hypobranchial is connected to the second basibranchial and the second and third hypobranchial are connected to the third basibranchial with an articulation process. They lie for the most part in a plane just ventral from the axis through the basibranchials. From dorsal and ventral view the hypobranchials are rod-shaped. In cross-section, these bones are thin and crescent-shaped, with the convex side dorsal.

Ceratobranchial. The ceratobranchials are similar to the hypobranchials (except number five, see below), only much longer. The first three are connected to the hypobranchials, while ceratobranchials four and five are connected to a patch of

cartilage which in turn is connected to the posterior end of basibranchial three. Ceratobranchial four is slightly different in having a small internal projection. The fifth ceratobranchial looks rather different, being flattened and widened and has a dorsal tooth patch fused to it. The fifth ceratobranchial is the only component of branchial arch number five. All ceratobranchials originate in the same plane as the hypobranchials but curve caudo-dorsad.

Epibranchial. The first four gill arches have an epibranchial connected to their ceratobranchial. The epibranchial makes a sharp angle with the ceratobranchial, thus creating a ventral and a dorsal branch of the gill arches. The first epibranchial is the longest; they decrease in size posteriorly. The epibranchial is basically similar in structure to the ceratobranchial and hypobranchial and they possess processes for articulation with the pharyngobranchials. The fourth, and sometimes the third, epibranchial is T-shaped.

Pharyngobranchial. The first four gill arches have a pharyngobranchial connected to the epibranchial. The first pharyngobranchial is a short rod-like bone that connects the branchial arch to the parasphenoid. The second, third and fourth pharyngobranchials are widened and flattened bones with tooth plates fused to their dorsal surface (the epibranchial and pharyngobranchial make an angle with the ceratobranchial, thus the dorsal side of the epibranchial and pharyngobranchial are oriented towards the ventral side of the individual; see Figs. 5.21a, b). The fourth "pharyngobranchial" is in fact the tooth plate alone, for the fourth pharyngobranchial is cartilaginous (Johnson, 1986). A small, block-shaped fourth pharyngobranchial cartilage is present (**character 30, state 0**) on the ventral surface of the pharyngobranchial tooth plate, in most perciforms, including all outgroup taxa (Fig. 5.22d). and absent (**state 1**) in all other groups considered here (Fig. 5.22c), including *Sphyraena*. See also character 7 of Johnson (1986). Of these three pharyngobranchials, the second is normally the shortest and the third the longest. In most perciform fishes, there is no direct bony contact between the third pharyngobranchial and the fourth pharyngobranchial tooth plate (Fig. 5.22a) (**character 31, state 0**). In the scombrids (except *Grammatorcynus*) and the billfishes, a triangular bony stay from the fourth pharyngobranchial tooth plate extends along the ventromedial side of the third pharyngobranchial (Fig. 5.22b) (**state 1**). Collette *et al.* (1984, character 3) mistakenly state that this stay extends from the third pharyngeal tooth plate, while Johnson (1986, character 31) correctly states it extends from the fourth pharyngeal tooth plate. Collette & Russo (1984) state that in *Acanthocybium* and *Grammatorcynus* this stay is shorter than in *Scomberomorus*. Probably, there has been some confusion between a long stay, an undulated margin and no stay. I accept subsequent reports that *Grammatorcynus* does not possess such a stay (Johnson, 1986 and Carpenter *et al.*, 1995). In the scombroids and *Sphyraena*, a remarkable articulation of the second epibranchial

and the third pharyngobranchial exists: the expanded tip of the second epibranchial articulates with the third pharyngobranchial through a long piece of cartilage that extends medially well beyond the midline of the third pharyngobranchial (Fig. 5.22c) (**character 29, state 1**). See also character 1 in Collette *et al.* (1984) and character 6 in Johnson (1986). In outgroups, the second epibranchial cartilage only abuts with the third pharyngobranchial (Fig. 5.22d) (**state 0**). One of the major factors why *Sphyraena* was accepted into the scombroids by Johnson (1986) must have been that it shares this "unique" articulation with "real" scombroids. Recent classifications, De Sylva (1984) and Nelson (1984) placed *Sphyraena* in a separate monogeneric suborder, closely related to the Mugilidae. Later, Nelson (1994) adopted Johnson's (1986) hypothesis that *Sphyraena* is a scombroid. The mugilids that I have included in this study do not possess this apomorphous articulation of branchial arch bones.

Gill rakers. The hypobranchial, ceratobranchial and epibranchial elements of the gill arches normally support one or more series of gill rakers. These are structures that prevent food loss through the opercular gap (Collette & Chao, 1975; Nakamura, 1991d). The first gill arch supports splint-like gill rakers (Fig. 5.21b), which are long, spine-like structures with a slightly widened basis. The splint-like gill rakers normally cover the whole of the first gill arch (**character 33, state 0**). Besides these, the first to fourth gill arches possess plate-like gill rakers, which are rounded, flat bony patches, each possibly bearing one or more cusps (Fig. 5.21c).

In the outgroup *Coryphaena*, as in some species of *Scomberomorus* and *Sphyraena,* and most gempylids, the number of splint-like rakers is strongly reduced (**state 1**). In those gempylids concerned there is just one splint-like raker left, in the angle between the ceratobranchial and the epibranchial. Any splint-like structures are cusps from the plate-like gill rakers. In the species of *Sphyraena* and *Scomberomorus* concerned, there is a range between one and nine splint-like gill rakers. In Collette *et al.* (1984) and Carpenter *et al.* (1995), the number of gill rakers on the first arch is counted or indicated. However, the spine-like structures on the first arch of trichiurids spring from plate-like gill rakers and are not solitary spines with a widened basis. In other words: trichiurids lack splint-like gill rakers and possess only plate-like ones with long cusps. The same condition is found in some gempylids, some species of *Sphyraena*, in *Acanthocybium*, *Gasterochisma* and istiophorids. In *Xiphias* there is a complete lack of gill rakers, either splint- or plate-like (**state 2**). Johnson (1986) made this a two-state character (no. 44): gill rakers present or absent. I follow here Carpenter *et al.* (1995, character 44) who give this character three states, as described above.

Two species of *Rastrelliger*, *Rastrelliger brachyosoma* (Bleeker, 1851) and *Rastrelliger kanagurta* (Cuvier, 1871), have gill rakers that are so long that they are visible through the open mouth (Fig. 5.21d). The remaining species of *Rastrelliger*,

Rastrelliger faughni Matsui, 1967 has slightly shorter rakers that are not visible through the open mouth (Matsui, 1967).

5.2.1.3 Billfish rostrum.

The billfishes *Xiphias* and the istiophorids have an elongated upper portion of the snout, formed by parts of the bones that normally form the upper jaw: the maxilla and premaxilla. Other components of the rostrum have long been the subject of discussion. Elements that have been recognised are the prenasal, nasal and ascending rami of the premaxillae. Other scombroids and outgroups concerned here lack this rostrum (**character 18, state 0**). Provisionally, the palaeorhynchids and *Blochius* which are fishes with rostra, are retained within the billfishes, although their systematic status is now uncertain (see § 7.3). The presence of the rostrum is expressed as character 13 in Collette *et al.* (1984) and character 46 in Johnson (1986).

There are a few fossil rostra, assigned to extinct billfish. Compared to Recent billfish, these are bizarre in every respect. The taxa in question are *Cylindracanthus, Congorhynchus* Dartevelle & Casier, 1949 (specimens not seen), *Hemirhabdorhynchus* and *Aglyptorhynchus*. Since it is doubtful that these rostra are of billfish (see § 7.3), here is not the place to describe the characters of these rostra and I refer to the chapter on Systematic Palaeontology (§ 7.3).

Shape in cross-section. The bill of *Xiphias* is dorsoventrally flattened (Fig. 5.23a) (**character 18, state 2**). The rostrum of Recent istiophorids is ovoid (Fig. 5.23b) (**state 1**). I have not seen cross-sections of *Blochius* rostra, but these are described in Schultz (1987). Dorsally it is convex, almost circular and ventrally it is only slightly convex, almost flat (Fig. 5.23c). Fierstine (pers. comm.) cannot confirm with absolute certainty the shape of the *Blochius* rostrum, but he suggested it might be somewhat rounded and ornamented with longitudinal grooves.

Length (character 19, states 0 and 1). In most billfish, the rostrum is considerably longer than the lower jaw (Fig. 5.24a). In *Tetrapturus angustirostris* Tanaka, 1915 and *Tetrapturus belone* Rafinesque, 1810 the rostrum is not much longer than the lower jaw, which is long as or shorter than the head. In other words, here the upper and lower jaw are almost equal in length and not much elongated. The rostrum is markedly elongated in the palaeorhynchids *Palaeorhynchus* and *Pseudotetrapturus* (Schultz, 1987), but these also have elongated lower jaws, so the upper and lower jaw are about equal in length (Fig. 5.24b).

Longitudinal channels. *Xiphias* and the fossil *Xiphiorhynchus* have a central canal (Fig. 5.23a, d), which is very wide in *Xiphias* (here called central chamber) and narrow and semi-circular in *Istiophorus* and *Xiphiorhynchus*. *Thalattorhynchus* Schultz, 1987 is characterised by a single eccentric canal through

the rostrum, but it is argued that this is not a new genus, but an unidentifiable istiophorid (Fierstine & Voigt, 1996). Recent genera of istiophorids have two nutrient channels. Schultz (1987) resurrects the genus *Pseudohistiophorus* De Buen, 1950, which is normally considered a synonym of *Tetrapturus* (Nakamura, 1985; Nakamura, 1983; Fierstine & Voigt, 1996). Schultz's diagnosis was based on sections of only one rostrum of *Tetrapturus angustirostris*, which was sectioned only where the premaxillae are still separated. I believe that the "central canal" which Schultz (1987, Fig. 3) indicates in "*P. angustirostris*" is an artefact of this incomplete way of collecting data. It is also likely that the two unusually large, axially placed nutrient channels in this "*Pseudohistiophorus*" are the fossae for the anterior extension of the maxillae (see also Fierstine & Voigt, 1996). Apart from the central canal, *Xiphiorhynchus* has two pairs of nutrient channels, of which the ventral pair is larger than the dorsal one. Since these characters seem to be useful mainly for identifying fossil taxa, they have not been used for the analysis of all scombroids.

Midline sutures. These are normally visible in istiophorids, except in *Istiophorus* and *Xiphiorhynchus* (compare Figs. 5.23b, d, e). Since these characters seem to be useful mainly for identifying fossil taxa, they have not been used for the analysis of all scombroids.

Nasal. Most authors accept that the nasals occupy the largest portion of the *Xiphias* rostrum (Gregory & Conrad, 1937; Nakamura, 1983; Nakamura, 1985) (Fig. 5.25a). However, Conrad (1937) found in juvenile *Xiphias* a small bone that he considers to be the nasal (Fig. 5.25b) and states the two large median bones in the rostrum of *Xiphias* are ascending rami of the premaxillae. Only Johnson (1986) seems to have followed Conrad's (1937) suggestion. I have not observed the bone which Conrad (1937) considers to be a nasal. Johnson (1986) claims to have observed this bone and he accepts Conrad's observation.

Prenasal. The prenasal is a bony element absent in most scombroids (**character 25, state 0**). It is found (**state 1**) in perciform outgroup taxa, like the carangid *Trachurus* (Fig. 5.26a) and in *Coryphaena*. Large bone elements in the rostrum of the bill of both istiophorids and *Xiphias* are debated to be prenasals. Gregory & Conrad (1937) and Nakamura (1985) state that the nasal in istiophorids is a short bone and the ascending processes of the premaxillae, being the dorsomedian bones of the bill, take up most of the rostrum. Schultz (1987) and Fierstine & Voigt (1996) however, find that these are not parts of the premaxillae, but are instead prenasals (Fig.5.26b, c). Schultz (1987) has even noted the presence of an internasal, a small paired bone between the nasal and the prenasal. The bones in the rostrum possess many wrinkles on the surface, making it somewhat difficult to see where the sutures between the different elements are located. A ventral view of a billfish rostrum however (Fig. 5.26d) shows that there is no internasal.

According to my observations, Fierstine & Voigt (1996) are correct: small nasals, no internasals and large prenasals. In *Xiphias* (Fig. 5.25), there is a similar problem. Fierstine & Voigt (1996) suppose that the median bones in the *Xiphias* bill, considered either nasals or ascending rami of the premaxillae (see description of nasal), can also be prenasals (see also Schultz, 1987), thus producing a rostrum topography that agrees more with that of istiophorids. If istiophorids and *Xiphias* are closely related, this topography with large median prenasals would be very likely for *Xiphias*. Both Johnson (1986) and Fierstine (in Fierstine & Voigt, 1996) have observed (a) juvenile cleared and stained specimen(s) of *Xiphias* and they state that there is no prenasal in one specimen of *Xiphias* that could be well observed (also Fierstine, pers. comm., 2000). Fierstine & Voigt (1996) suggest investigating more larval *Xiphias* before generalising this condition. Unfortunately, unlike with istiophorids, I have not had the opportunity and the appropriate specimens to study the *Xiphias* bills up to the same detail as the istiophorid bills. Although I tend to accept the nasal as a small bone in *Xiphias* and the absence of prenasals, more detailed and better reported research on this discussion would resolve the question. The supposed absence of prenasals means that the large median bones in *Xiphias* bills are ascending rami of the premaxillae.

5.2.2 Vertebral column

5.2.2.1 General characters.

The vertebral column consists of a series of vertebrae. The anteriormost vertebra is connected to the head through articulation with the basioccipital. Only in the Thunnini is the first vertebra fused to the basioccipital. The last few vertebrae are modified to form the caudal skeleton. The vertebral column can be divided into two sections: the precaudal and the caudal (Fig. 5.27a, b). The precaudal vertebrae form the rostral part of the vertebral column and are characterised by the possession of ribs on all but the first few vertebrae. The caudal section of the vertebral column is characterised by heamal arches which bear long spines (§ 5.2.2.4) ventral to every vertebra, and a lack of ribs. The bone which bears the first element of the anal fin (pterygiophore) is normally loosely connected to the first long haemal spine, except in istiophorids, where the posterior section of a double anal fin is loosely connected to the distal end of the vertebral column (Fig. 5.27b). The first caudal vertebra is preceded by either a precaudal vertebra without ventral spine or with a much shorter one (see description of vertebrae and Fig. 5.27). The vertebral count in the studied taxa shows enormous variability, from 23 in some specimens of *Sphyraena* and in luvarids, to 174 in *Trichiurus* (**character 38, states 0, 1 and 2**). Collette *et al.* (1984, character 29), Johnson (1986, character 16) and Carpenter *et al.* (1995, character 16) also used a vertebral count-character. After my observation and including the fossils, I have divided this character in

different classes. Collette *et al.*'s states of their character 29 are: 0: 24-26, 1: 30-31, 2: 35-170. Johnson's states of his character 16 are: 0: 24-26, 1: 30-31, 2: 32-67, 3: 98-192. Carpenter *et al.*'s states of their character 16 are: 0: 24-26, 1: 30-55, 2: 58-67, 2: 98-192. Collette & Russo (1984) also have a vertebral count character (number 27) for Scomberomorini. The states of my **character 38** are: **0**: 23-26, **1**: 28-64, **2**: 76-174. The main body of the vertebra is the centrum. Besides the centrum, a vertebra may consist also of parapophyses, the neural and haemal arch and their appendages: the neural and haemal spine and the zygapophyses (Figs. 5.28a1-3).

5.2.2.2 Centrum.

The centrum, the central, and largest element of the vertebra, is a short or long biconcave (amphicoelous) bone, with a diameter that is rather ovoid, with the long axis either horizontal or vertical, depending on the taxon and the position of the vertebra in the vertebral column. In the outgroup *Scombrolabrax*, the parapophyses (see description of haemal arch) are modified in vertebrae 5 to 12. These parapophyses bulge dorsolaterally to form pocket-like bullae (**character 44, state 1**) that open ventrally (Bond & Uyeno, 1981 and Fig. 5.28b). Delicate bubble-like outgrowths of the swimbladder (gas bladder) fit into these pockets. These bullae are absent in other groups (**state 1**). Bond & Uyeno (1981) do not comment on the function of this remarkable structure. In lateral view, the centrum is approximately hourglass-shaped, with the narrow middle part mostly wider than 30 % of the maximum width of the centrum (**character 39, state 0**). Only in the billfishes does the narrow part of the centrum seem to be narrower than 30 % of the maximum centrum diameter (Fig. 5.28c1) (**state 1**). The centra of istiophorids also possess a lateral keel, the lateral apophysis (lateral apophysis: Nakamura, 1983; Davie, 1990; transverse flanges: Fierstine (1974); lateral keel in *Trachurus*: Suda, 1996). This keel is rather narrow in *Istiophorus* and *Tetrapturus* and is not conspicuously visible in dorsal or ventral view. In *Makaira* however, the lateral apophysis is anteriorly widened, about as wide as the diameter of the centrum (Fig. 5.28c2). The centra generally bear two lateral depressions: one dorsal and one ventral. In most groups, a mid-lateral depression is absent (**character 40, state 0**), but in †*Scomberodon* there is a small midlateral depression (**state 1**) and in *Acanthocybium* there is also a midlateral depression (Fig. 5.28d).

5.2.2.3 Neural arch.

The neural arch is, as the name says, an arch-like structure on the dorsal side of the vertebral column, that extends around the spinal cord. Every centrum possesses a neural arch. All these neural arches together form ta larger arch covering the whole vertebral column. From the apices of these arches, spine-like

(**character 44, state 0**) processes extend: the neural spines. The neural spines of *Xiphias* are somewhat blunt-tipped, flattened and broadened into a plate-like appearance (Fig. 5.28e) (also coded as **state 0**). In istiophorids, the neural spines are bizarrely modified into large, parallelogram-shaped plates, pointing posteriorly (**state 3**). In *Coryphaena* the neural spine is bifurcated into two prongs of unequal length (**state 1**). In the palaeorhynchids the neural and haemal spines have an oval distal outgrowth (Fig. 5.28f) (**state 2**). In some specimens of lesser preservation quality, the distal haemal plate appears as a distal spine, thus resembling **state 1** of **character 44**.

5.2.2.4 Haemal arch.

The haemal arch is a structure similar to the neural arch, extending ventrally around the caudal artery and vein. One difference from the neural arch is that in the first few vertebrae the haemal arch is not closed; instead there is a pair of small haemal plates: the parapophyses (Fig. 5.28a1) (basapophysis: Suda, 1996; parapophysis: Bond & Uyeno, 1981; Collette & Nauen, 1983; Collette & Russo, 1984). These serve solely for rib articulation (except in *Scombrolabrax*, see above). Further posteriorly, these haemal plates grow larger and closer together to ultimately form the haemal arches (Fig. 5.28a2). The first few spinescent haemal arches bear only small spines. The start of the caudal part of the vertebral column is marked by a sudden lengthening of the haemal spines (Fig. 5.27) and the absence of ribs. Using De Sylva's (1955) terminology, the first vertebra with a closed haemal arch is not the first caudal vertebra. The first few centra with closed haemal arches may bear a short ventral rod, but not a long spiniform structure. The first centrum with a long haemal spine is here counted as the first caudal vertebra. The anal fin articulates with the first caudal haemal spine except in Istiophoridae, where the anal fin does not seem to articulate with the axial skeleton.

Laterally, haemal arches normally have small inferior foramina. In the tunas *Auxis*, *Euthynnus* and *Katsuwonus*, and the yellowfin group of *Thunnus*, a few of the posterior haemal arches possess markedly enlarged inferior foramina (Fig. 5.29a-c), an adaptation for the neothunnoid heat exchanger (**character 77, state 3**) and its central network of *retia mirabilia* (see § 4.1). Another adaptation to the neothunnoid exchanger is a wider and more rounded haemal arch than seen in other scombroids. Graham & Dickson (2000) mention a modified central circulation and enlarged or otherwise modified haemal arch as their "new character 1". Although it is uncertain whether the small heat exchanger in *Allothunnus* is sufficient to conserve enough body warmth for systemic endothermy, the basic adaptations are present in *Allothunnus*. Therefore, this character is coded 3 for the cladistic analysis. The bluefin group of *Thunnus* do not possess these above mentioned adaptations. As mentioned in § 4.1, these species have a so-called

thunnoid heat exchanger, which lacks the central network of *retia mirabilia* **(character 77, state 4).**

The mackerels *Rastrelliger* and most species of †*Scombrinus* (also known as *Auxides* Jordan, 1919 and *Scombrosarda* Danil'chenko, 1962; see Systematic Palaeontology) have a first haemal spine which is thickened and bent in a sickle-shaped way (Fig. 5.30a). The spine seems to be more widened in *Scombrinus* than in *Rastrelliger* (Fig. 5.30b). The degree of curvature of this spine is one character to distinguish between different species. In the other mackerel, *Scomber*, the first haemal spine is bent in an S-curve (Fig. 5.30c). This condition is also found in †*Abadzekhia*. In other scombroids and outgroups there is not such an obvious curvature as in mackerels (Fig. 5.30d). While these characters are mostly useful for species determination, they are less so for genus identification, and they are therefore not used in this phylogenetic analysis.

5.2.2.5 Zygapophyses.

Zygapophyses are the paired rostral and caudal outgrowths of the neural and haemal arch. Zygapophyses can be subdivided in prezygapophyses and postzygapophyses. The prezygapophyses spring from the haemal arch just anterior to the spine and the postzygapophysis just caudal to the spine (Fig. 5.28a3). Normally, the prezygapophysis is somewhat bigger than the postzygapophysis. In some taxa, namely in Thunnini, Sardini and Scomberomorini, the margins of the postzygapophysis develop into small fringes. The prezygapophysis interlocks with the postzygapophysis of the preceding vertebra. In *Xiphias*, the neural prezygapophysis is clearly bigger than the postzygapophysis; their haemal zygapophyses have hardly developed (Fig. 5.28e). In istiophorids the prezygapophyses are not only much larger than the postzygapophyses, but they are also modified into horizontally oriented, laterally flattened plate-like spines, about as long as the centrum (Fig. 5.28c1). These prezygapophyses do not interlock with the small inconspicuous postzygapophyses, but with the large, modified neural or haemal spine. A pair of these prezygapophyses acts as a two-way fork into which the preceding spine is locked (Fig. 5.28c2). The prezygapophysis interlocks with the preceding neural spine from the first neural spine onward in all but a few specimens. On the ventral side of the vertebral column, the interlocking starts at the first haemal spine. This interlocking structure continues dorsally and ventrally until the posteriormost vertebra. These specialisations in the istiophorid vertebral column result in a rigid structure, but apparently there is still enough flexibility in the vertebral column to permit movement in the horizontal plane, since billfishes swim in the undulatory "carangiform" mode (see § 4.2). Nakamura (1983) suggested that this prezygapophysis-vertebral spine chain acts as a spring for their jumping behaviour: billfish are known to leap very high above the surface of the water, as

dolphins do. Fossil billfish (palaeorhynchids) also have a modified vertebral column, although only in the spines (Fig. 5.28f). Palaeorhynchids have an elongate snake-like body, in that sense resembling some gempylids. Fishes with that swimming mode are expected to have an undulatory mode of swimming (compare with Nakamura (1992, 1993a). It is hypothesised that the plate-like expansions of palaeorhynchid spines serve for muscle attachments and in the Recent billfish these structures have been modified further and have evolved, together with the prezygapophyses, into a structure with the added function of a spring for jumping behaviour. These adaptations of the zygapophyses have co-evolved with the neural and haemal spines of billfishes, and therefore do not need to be included separately in the phylogenetic analysis.

5.2.2.6 Bony caudal keel.

Scombrids possess a fleshy keel at the peduncle of their tail (see description of soft-tissue characters). Only in Sardini and Thunnini is a bony support for this keel is found, but not in other groups (**character 46, state 0**). The bony keel is built up of modified transverse processes of the last few vertebrae preceding the caudal skeleton (Fig. 5.31a-c). It is said generally, that the keels in Sardini are incomplete and not well-developed (Fig. 5.31b) (**state1**) and that in the Thunnini (Fig. 5.31c) they are larger and well developed (**state 2**). The distinction between the development of the keel in Thunnini and Sardini is blurred by the systematic position of *Allothunnus*, generally recognised as a bonito (as in Collette, 1978; Collette *et al.*, 1984 and Collette & Nauen, 1983). As in bonitos, *Allothunnus* possesses a narrow and incomplete bony caudal keel. Collette *et al.* (1984) suggested that *Allothunnus* be considered a Sardini. Graham & Dickson (2000) have found evidence that confirms *Allothunnus* as the most primitive Thunnini. Whether *Allothunnus* is a Thunnini or a Sardini (see phylogenetic analysis, Chapter 8), the narrow emarginated keel is plesiomorphous relative to the wide and completely margined keel as seen in (most) Thunnini. Characters of this caudal keel have been used before: Collette *et al.* (1984, character 17).

5.2.3 Caudal skeleton

5.2.3.1 General characters.

The caudal skeleton (Fig. 5.32) of fishes consists of modified vertebrae. One of the functions of the caudal skeleton is to provide support for the lepidotrichia of the tail fin. The largest portion of the caudal skeleton, which also provides the most support to the caudal fin, consists of the hypural elements (Fig. 5.32a, example of non-scombroid fish with all the discussed elements autogenous). These hypural bones are modified, enlarged haemal spines, and in the studied groups there are generally five of them. A smaller portion of the tail is supported by epural bones

(Fig. 5.32a). The hypural and epural bones are in turn supported by the ural vertebra, which is modified in scombroids (see description of urostyle). Some support is also provided by preural vertebrae 2-4 (preural centrum 1 has become part of the caudal complex, see § 5.2.3.3). The trichiurids *Eupleurogrammus*, *Lepturacanthus* and *Trichiurus* are characterised by the complete absence of a caudal skeleton (**character 49, state 1**). Senta (1975), Nakamura (1993b) and Gago (1998) described a reduced caudal complex in *Tentoriceps*. The specimen I x-rayed (BMNH 1974.3.5.1) does not show whether that reduced caudal complex is present or not. Other trichiurids and every other taxon in this analysis possess a fully developed caudal complex (**state 0**). The reduction of the caudal complex is used in Gago's (1997, character 8; 1998, character 56) analyses of trichiurids.

5.2.3.2 Hypural elements.

In most outgroups, such as *Scombrolabrax*, and sphyraenids, the caudal skeleton is not specialised and shows the general condition, with five autogenous hypural elements (**character 53, state 0**). In Luvaridae however, the caudal skeleton is modified in such a way that it resembles that of scombrids (see below). In scombroids, the caudal skeleton is highly specialised and modified. In "lower" scombroids such as trichiurids and Scombrini, and the studied mugilids, fusion has taken place between hypural elements 1 and 2 ventrally and 3 and 4 dorsally (see Fig. 5.32b, c) Thus, they effectively possess two small hypural plates: a dorsal one, consisting of hypurals 3 and 4, and a ventral one, consisting of hypurals 1 and 2 (**character 53, state 2**). In gempylids, fusions in the dorsal and ventral region of the hypural plate happen independently of each other and with relatively great variety. There are gempylids with two small hypural plates (*Diplospinus* and *Paradiplospinus*, see Russo, 1983), as in Scombrini and trichiurids. Other gempylids have their hypurals 1 and 2 free, while hypurals 3 and 4 are fused into a small plate (**character 53, state 1**), as in *Gempylus* (Fig. 5.32d) and *Nealotus*; again others have a caudal complex with all elements autogenous. In the "higher" scombrids (all scombrids but the Scombrini, as in Fig. 5.32b), hypural elements 1-4 are fused into a single hypural plate (Figs. 5.32e-h). The fusion pattern of the hypural elements and the presence or absence of the caudal notch have been expressed before in Russo (1983, characters 79-81, 83), Collette *et al.* (1984, characters 32-35) and Johnson (1986, characters 13 and 39). Johnson (1986) makes some incorrect assumptions on the hypural fusion pattern (see also § 5.1) and does not consider the absence or presence of the caudal notch as a character. The fifth hypural is normally a loose element in a teleost caudal skeleton (Fig. 5.32a). In the scombroids there are several exceptions to this rule. The fifth hypural is completely fused to the hypural plate (**character 54, state 2**) in some gempylids (*Diplospinus* and *Paradiplospinus*: see Russo, 1983; 1986; Carpenter *et al.*, 1995).

In *Scomber* (Fig. 5.32b) and *Rastrelliger* the fifth hypural is completely fused to the uroneural, but not to hypural 4 (Potthoff, 1986). This also seems to be the case in †*Scombrinus*. In palaeorhynchids (Fig. 5.32i), *Lepidocybium*, the Sardini and Thunnini (Fig. 5.32f, g) the fifth hypural is partially fused (**character 54, state 1**) to the hypural plate; in trichiurids it is completely fused to the plate (Fig. 5.32c). In the istiophorids (Fig. 5.32j), the fifth hypural is missing altogether (**character 54, state 3**); it is known to disappear in the ontogeny of the Recent taxa (Ovchinnikov, 1970; Collette *et al.*, 1984; Potthoff *et al.*, 1986) and is not found in any of the fossil taxa. In most fossil hypural plates, one could make assumptions whether all five hypurals are fused or whether the fifth hypural has not developed, depending on the phylogenetic affinities of the fossil. However, making such estimates is hazardous, so in fossils where this is not clear, the status of the fifth hypural is coded as ambiguous in the data matrix. Nakamura (1983, Fig. 12) and Nakamura (1985, Fig. 13) erroneously show five hypural bones in *Istiophorus*. I follow Potthoff's (1986) observations on the ontogenetic development of scombroids. The fifth hypural fuses to the hypural plate early in the ontogeny of the trichiurids with a caudal complex. I am unsure how to code this character in *Grammatorcynus*. Collette & Russo (1984) note that the fusion of the fifth hypural to the plate depends on the size of the specimens. There is no indication whether this is correlated with maturity or not. The fusion of the fifth hypural is character 35 in Johnson (1986). In most scombroids, the hypural complex possesses a caudal notch (Figs. 5.32b-e, i, j) (**character 53, state 3**), which indicates the division between hypurals 1-2 and 3-5 respectively. In Recent *Gymnosarda* this notch is reduced to a small inconspicuous vestige (Fig. 5.32h) (**character 53, state 4**). The fossil *Gymnosarda prisca* Monsch, 2000 has a conspicuous caudal notch (see Monsch, 2000 and § 7.3). In other Sardini and all Thunnini, this caudal notch is absent (Figs. 5.32e, f) (**character 53, state 5**).

5.2.3.3 Urostyle.

The urostyle is the bone element preceding the hypural plate (Fig. 5.32a). It is a fusion of two elements: the preural centrum 1 and the ural centrum, following the terminology of Potthoff (1975). Thus, the first free vertebra preceding the caudal skeleton is Preural 2. The urostyle is separate from the hypural plate in most scombroids. In scombrids other than *Scomber* and *Rastrelliger*, and in the billfishes, the urostyle has fused with the hypural plate and has become part of it. This character has not been used in the phylogenetic analysis. There are already many caudal region characters included and there are other characters that identify the taxa in question.

5.2.3.4 Uroneural.

Uroneurals are bones that are characteristic of teleost fishes. They evolved from the neural arches of the caudalmost tail vertebrae, several of whose arches moved forward to overlie the base of the caudal skeleton. At the same time, modification of their morphology took place, towards a splint-like shape: uroneurals (Maisey, 1996) (Fig. 5.32a). Gempylids possess two uroneurals, just as the outgroup taxon *Scombrolabrax*. Other scombroids have only one uroneural. While in most scombroids the uroneural is autogenous, in istiophorids, Sardini and Thunnini the uroneural is fused to the hypural plate (Fig. 5.32f-h, j). The uroneural is clearly visible in Sardini and Thunnini by an anterodorsal projection on the hypural plate, but this cannot be seen in istiophorids. It is the study of scombroid ontogeny by Potthoff (1986) that supplies data of these fused elements. Characters of the uroneural have not been used in the phylogenetic analysis. There are already many caudal region characters included and there are other characters that identify the taxa in question.

5.2.3.5 Parhypural.

The parhypural is the caudalmost haemal spine and is normally autogenous. Its dorsal apex develops into two lateral processes, one of which points anteriorly, one posteriorly. These two dorsal processes of are together called the parhypurapophysis. Normally autogenous (**character 55, state 0**) (Fig. 5.32a-g), the parhypural is fused to the plate (**state 1**) in istiophorids and palaeorhynchids (Fig. 5.32i, j), *Acanthocybium* and *Gymnosarda* (Fig. 5.32h). There have been reports that in *Scomberomorus niphonius* (Cuvier, 1831) and *Scomberomorus plurilineatus* the parhypural is also fused to the hypural plate (Uyeno & Fuji, 1975; Collette & Russo, 1984). Collette & Russo (1984) mention that the parhypurals of those species are partially fused to the hypural plate. In specimens of *S. plurilineatus* (USNM 264809 and 269760) and *Scomberomorus niphonius* (BMNH 1874.1.16.9 and 1890.2.26.90) the parhypural does not seem to be fused to the hypural plate. The fusion of the parhypural has been used as a character before (Collette *et al.*, 1984: character 36; Johnson, 1986: character 45).

5.2.3.6 Epurals.

In perciforms and most scombroids, three epurals develop (**character 52, state 0**). Luvarids seemingly have no epurals, but studies by Tyler *et al.* (1989) show that three epurals develop in their ontogeny, which all fuse into one structure which in turn is fused with the second preural centrum. Scombrids, *Eocoelopoma* and *Palimphyes* have two epurals (**state 1**). This is character 7 of Collette *et al.* (1984) and character 36 of Johnson (1986). In the Thunnini, there is seemingly just one epural (Fig. 5.32f, g), but there are really two. The most anterior of its

epurals is fused with the neural arch of preural centrum 2 (Collette *et al*, 1984). Thus, the neural spine that preural centrum two seems to have is the second epural. Preural centrum 2 does not bear a neural spine. Within gempylids, *Diplospinus* and *Paradiplospinus* have only two epurals (Russo, 1983). Trichiurids have a single epural (Fig. 5.32c) (**state 2**). Both Collette *et al.* (1984) and Johnson (1986) seemed to have ignored in their phylogenetic analysis that trichiurids have only one epural. Billfishes have three epurals, although they have been reported to have two (Nakamura, 1985, Fig. 13). However, Nakamura's (1985) "autogenous neural spine" really is the third epural and the "uroneural" is the first. Ovchinnikov (1970) also recognises only two epurals in istiophorids. I have accepted Potthoff *et al.*'s (1986) study of the ontogeny of scombroids, which states that billfishes have three epurals. Davie (1990, Fig. 9) has correctly observed and figured this presence of three epurals, as has Nakamura (1983) in earlier work.

5.2.3.7 Preural centra.

In Sardini and Thunnini, but most notably in the Thunnini, there is a sudden shortening of the last two or three centra (Fig. 5.32g) (**character 43, state 1**), which is not seen in the other taxa (**state 0**). In a thus far undescribed fossil billfish (see § 7.3) and *Palaeorhynchus*, the neural and haemal spines of the last few vertebrae are laterally flattened, and widened into a fan-shaped structure (Fig. 5.32i, k) (**character 44, state 1**). In other taxa, the neural and haemal spines are spiniform (**state 0**), although in some cases somewhat widened in and flattened (Fig. 5.31).

5.2.4 Appendages

5.2.4.1 General characters.

The appendages can be divided into the unpaired fins (predorsal bones, first and second dorsal, anal and possibly second anal, caudal fin, dorsal and anal finlets) and the paired fins (pectoral and pelvic fins and their respective bony girdles). In the trichiurids, both dorsal fins are united into one continuous fin. In *Benthodesmus* and *Aphanopus* there is a clear notch which clearly marks the change of the first into the second dorsal fin. Otherwise, the distinction between the first and the second dorsal fin is made through the rigidity of the fin elements (see below). In the outgroup taxon *Coryphaena* and the enigmatic *Blochius*, there seems to be just one long, continuous dorsal fin, without a distinction between two sections (**character 69, state 0**).

5.2.4.2 Predorsal bones.

The presence of predorsal bones (**character 60, state 0**), is a normal feature in my chosen outgroup taxa (except *Scombrolabrax* and *Coryphaena*) and other percoids. In most recognised scombroids, the predorsal bones are absent (**state 1**). This is character 2 of Collette *et al.* (1984) and character 11 in Johnson (1986). The fact that *Gasterochisma* possesses three well-developed predorsal bones fuels the suspicion that it is not a scombroid. Three gempylid genera: *Ruvettus*, *Thyrsitops* and *Tongaichthys* are reported to have one predorsal bone. (Potthoff *et al.*, 1986). The presence of this predorsal bone in *Ruvettus* was determined using specimens of 209 and 212 mm (Potthoff *et al.*, 1986). However, a 350 mm specimen (BMNH 1938.6.23.24) possesses no predorsal bone. I believe that more research is needed to confirm to what degree predorsal bones develop in the various gempylid taxa and whether it is certain that this bone is present in fully grown adults. Because of this ambiguity, the state "one predorsal" for character 60 is not considered here. There seems to be a sharp division though, between taxa having three and zero (and possibly one) predorsals, so this two-way division is upheld here. *Sphyraena* possesses three bone elements that are situated anterior to the first dorsal fin, but these are not homologous with real predorsal bones. "Real" predorsal bones are simple, separate structures of which the first is inserted in the first interneural space (Fig. 5.33a). In *Sphyraena* however, these so-called predorsal bones have a more complex structure, as the bearers of (dorsal) fin rays, and the first one is inserted in the second interneural space. Furthermore, these three bones interlink as ray bearers do. Because of this, Johnson (1986) argued that these structures are degenerate first dorsal ray bearers. I propose here the term pseudo-predorsals to describe these structures. The mullets also possess pseudo-predorsals, albeit somewhat different from those in sphyraenids. In the mugilids, these bones, except the third, have the same "complex" structure as in *Sphyraena*. The third pseudo-predorsal of the mullets is somewhat further "degenerated" than the first and second.

5.2.4.3 Dorsal fins.

Normally, there are two dorsal fins that are separately discernible and close together (**character 64, state 0**). In the Recent mackerels *Scomber* and *Rastrelliger* and the tuna *Auxis* however, the two dorsal fins are well separated (**state 1**). The space between the dorsal fins is filled with pterygiophores that do not bear fin rays or spines (Fig. 5.34a). In the fossil mackerel *Scombrinus* the dorsal fins are close together. In *Xiphias* the dorsal fins are also widely separated, but the space between the fins is not filled with rayless pterygiophores (Fig. 5.34b). In trichiurids, the two dorsal fins are continuous or only separated by a small notch (Fig. 5.34c) (also coded as **state 0**). In palaeorhynchids, there is also

one continuous dorsal fin, which can be divided into a "first dorsal" and "second dorsal" section (another variety of **state 0**). In Recent billfishes, separate dorsal fins are present, but juvenile specimens also have one continuous dorsal fin (Fig. 5.34d), like their fossil relatives.

First dorsal. Normally, the first dorsal fin consists of rigid spines (**character 65, state 0**). In billfishes and *Coryphaena* however, the first dorsal fin mostly to completely consists of soft rays (**character 65, state 1**). This is character 48 of Johnson (1986). All first dorsal rays of *Xiphias* are soft, with open bases. Nakamura (1985, Fig. 7), divided the first dorsal fin of istiophorids into three sections: three anterior fin spines, followed by nine soft branched rays, and about 30 fin spines without branched apices (Fig. 5.35). I have found, by my own observations, that these 30 fin "spines" are also soft structures, even though they are different from the preceding branched rays. Johnson (1986) argues that the first three fin spines are only secondary spinous rays and thus not homologous with true spinous dorsal fin rays. This is supported by the fact that all dorsal fin elements in juvenile specimens seem to be soft.

If in doubt, soft rays and hard spines can be distinguished by the morphology of their bases: that of hard spines is closed with a foramen for articulation, and with soft rays the base is completely open (Fig. 5.35b).

In percoids and scombrids, the ray-bearer of the first dorsal fin element, or pterygiophore, is inserted in the third interneural space (Fig. 5.33) (**character 61, state 0**). In taxa with pseudo-predorsals, *Sphyraena*, and mugilids, I have taken the insertion of the first pseudo-predorsal as the insertion of the first dorsal fin element. In *Sphyraena*, the first pseudo-predorsal is inserted in the second interneural space, and the first "real" first dorsal fin element is inserted in the fourth or fifth interneural space (Fig. 5.33a). In mullets, the first pseudo-predorsal is inserted in the third interneural space; the first "real pterygiophore is inserted as far posteriorly as the eighth interneural space. In gempylids and trichiurids, the first pterygiophore is inserted in the second interneural space (**character 61, state 1**). In the fossil *Palimphyes*, the first pterygiophore is normally inserted in the third interneural space, except in *Palimphyes chadumicus* Danil'chenko, 1960, in which the first pterygiophore is inserted in the fifth space (**character 61, state 2**). In the fossil mackerel *Scombrinus*, the first dorsal ray element is inserted in either the third or fifth interneural space. In *Xiphias*, it is inserted in the second or third interneural space and in the fossil billfish *Pseudotetrapturus* in the fourth or fifth space. In Recent istiophorids, *Blochius* and the outgroup taxon *Coryphaena*, the first pterygiophore is inserted in the first interneural space (in fact, the first pterygiophore is situated just dorsal to the skull). According to Potthoff *et al.* (1986), the first pterygiophore is inserted in interneural space 2 in the Sardini. My

observations of specimens of *Sarda* do not support this: it is inserted in the third interneural space. Johnson (1986) created a two-state character 19: first pterygiophore inserted in the third or in the second interneural space.

A synapomorphy of gempylids and trichiurids is the modification in the radials (elements of the pterygiophore) of the spinous and soft dorsal fins. While in most groups the proximal-middle and distal radials of the pterygiophore of the spinous dorsal fin overlap only slightly, in gempylids and trichiurids this overlap is extensive (compare Figs. 5.35c1-3). This is Johnson's (1986) character 21. Another of Johnson's (1986: character 22) synapomorphies of trichiurids and gempylids is that in these groups the distal radial snugly locks on to a process on the proximal-middle radial. This fine interlocking system is absent from other groups considered. Johnson treats the latter two characters as separate, but it would have been better to treat them as a single compound character, because one seems to lead to another: the fact that the distal radial locks tightly on to the proximal-middle radial, is probably part of the reason for the great overlap of these elements. Thus, my **character 62, state 0** indicates pterygiophore radials that do not overlap greatly and are loosely connected, **state 1** indicates pterygiophore radials that overlap extensively and snugly fit into each other. In the outgroup taxon *Luvarus* a similar neatly interlocking chain pf pterygiophores exist.

In *Xiphias*, *Makaira* and some species of *Tetrapturus* the first dorsal fin has an anterior lobe which is more than twice as deep as the remainder of the fin (**character 66, state 0**) (Fig. 5.35d). Most *Tetrapturus* have an anterior lobe which is not more than twice as deep as the rest of the fin (Fig. 5.35e) (**state 1**). In *Istiophorus*, the anterior lobe is not the highest point of the fin (Fig. 5.35a) (**state 2**). In other scombroids and outgroups, the first dorsal fin may be deeper anteriorly than posteriorly, but a clear anterior lobe is not discernible (Fig. 5.35f) (a variety **of state 1**).

The number of first dorsal fin elements (spines or rays) varies greatly. I have divided the variation (**character 67**) into four classes: 2-23 (**state 0**), as in louvars, *Trachurus*, *Sphyraena*, some trichiurids, most gempylids and all scombrids; 30-51 (**state 1**), as in *Gempylus*, *Xiphias* and istiophorids, 58-71 (**state 2**) as in *Coryphaena* and *Palaeorhynchus* and 97-107 (**state 4**) as in *Homorhynchus*. The amount of spines in the first dorsal fin is also used in a phylogenetic analysis of trichiurids (Gago, 1998).

Second dorsal. The second dorsal fin always consists of soft rays supported by pterygiophores. In the plesiomorphous condition, present in the outgroup taxa *Trachurus*, *Valamugil* and *Liza*, in *Sphyraena* and many scombroids, the soft rays are preceded by one or two second dorsal hard spines (**character 70, state 1**). In the scombroid taxa that have retained the rigid spines, *Dicrotus* has one or two and

†*Thyrsion* has two. Other taxa which have not lost their spine have only one. The scombroids that have lost their second dorsal spine(s) (**state 0**) are the trichiurids, the gempylid *Thyrsites*, the fossil *Palimphyes*, the billfishes, Scomberomorini, Sardini and Thunnini (except *Katsuwonus*).

Gago (1997) provided evidence that suggests that soft dorsal-pterygiophore elements in the trichiurids which seemingly correspond to those in gempylids and other scombrids do not. The proximal and middle radial are not fused in trichiurids, hence the two elements that strongly overlap and snugly fit into each other are the proximal and the middle radial. I will accept, for the phylogenetic analysis, the suggestions of Gago (1997). While the interlinked bony supports of the gempylids and trichiurids are analogous, they cannot thus be considered homologous. Potthoff *et al.* (1986) and Johnson (1986, character 30) noticed that the open basis of the soft dorsal and anal fin ray of trichiurids and embraces a (neomorph?) distal element (Fig. 5.35c3). Probably because the homology of the element was not clear, the above named authors did not properly name it. Johnson (1986: 21) referred to it as "additional distal radial" and "extra distal radial" (Johnson's quotation marks). Potthoff *et al.* (1986) also notice the presence of this element, and cannot indicate its homology to any other known bone. In their figures that show this element, Potthoff *et al.* (1986) and Johnson (1986) labelled the element with an "x". Subsequently, Gago (1997, 1998) refers to it as the "x" element. However, after first discussing this element as the "x" element, Gago (1997) provides evidence from his own larval studies, that seemingly corresponding elements are not homologous (see description of first dorsal). Thus, the "x" element should be considered the distal radial. The soft dorsal fin of gempylids is also supported by a small distal radial, embraced by the fin ray (Gago, 1997). I presume this element to be small and inconspicuous in gempylids; I even failed to see it in the studied gempylid specimens. If the suggestion that element "x" is the distal radial is accepted, and the main body of the pterygiophore consist of an unfused proximal and a middle radial (see above), then a synapomorphy of the trichiurids is still the presence of three autogenous radials (**character 62, state 1**), but then in a different configuration than previously thought (Potthoff *et al*, 1986; Johnson, 1986) and without neomorphs. In other groups, the soft dorsal fin is supported by two autogenous radials: the proximal-middle radial (an ontogenetic fusion of the proximal and middle radial) and the distal radial (**state 0**). Gago's (1997, character 3; 1998, character 50) configuration of elements of the pterygiophore, accepted here, is similar to that of the pterygiophores of the additional unpaired finlets in *Thunnus* Potthoff (1975), where three separate radials are present. The spinous dorsal fin pterygiophore in trichiurids is not so modified; it consists of the proximal-middle and distal radial. In the spinous dorsal fin, the distal radial resembles that of the gempylids and is not embraced by the dorsal fin

spine (Figs. 5.35c2, 3). At this point, Johnson's (1986) Figs. 8-9 are confusing. Although these figures concern spinous fins, for trichiurids soft fin elements (the "x" element present, fin ray with open basis) are figured.

The pterygiophore of a soft dorsal fin ray is normally not closely associated with a particular neural spine (**character 63, state 0**) of the vertebral column (Fig. 5.36a), except in the trichiurid subfamilies Lepidopinae and Trichiurinae (*cf.* Tucker, 1956) each second dorsal pterygiophore is fully associated with each neural spine just ventral to the second dorsal (**state 1**) (Fig. 5.36b). The fossil trichiurid *Anenchelum* closely resembles *Lepidopus* (subfamily Lepidopinae), but lacks the apomorphy of a close association of the soft dorsal fin with the vertebral column. Hence, *Anenchelum* does not fit in the classification based on Recent taxa. The phylogenetic position of *Anenchelum* is discussed in Chapters 7 and 8.

I have divided the ray count of the second dorsal into the following classes: 98-108 (**character 69, state 1**) in most trichiurids, 29-54 (**state 2**), as in *Trachurus, Aphanopus* and *Anenchelum*, 7-23 (**state 3**), as in *Sphyraena*, gempylids and scombrids. The istiophorids and *Xiphias* also possess second dorsal fins, but I argue below that these are not homologous with those of other taxa. The billfishes thus, together with *Coryphaena*, have no true second dorsal fin and a long soft first dorsal instead (**state 0**).

Finlets. Finlets are short, wide soft fin rays that are distally fimbriated into a brush-like structure (Fig. 5.37a). In the taxa where they occur there is a series of dorsal and ventral (anal) finlets. In early larval stages the second dorsal and the anal fin are long and continuous, but later on in the development in some taxa, separate finlets are isolated. The number of dorsal and anal finlets is mostly the same, although there is sometimes a difference of one finlet in the dorsal and anal fins. Finlets are absent (**character 74, state 0**) in all outgroup taxa. Within scombroids they are found in scombrids and in the gempylid genera *Gempylus*, *Lepidocybium*, *Nealotus*, *Nesiarchus*, *Dicrotus*, *Rexichthys*, *Ruvettus, Thyrsites, Thyrsitops and Tongaichthys* (pers. obs. and Nakamura & Parin, 1993). I consider the "second dorsal" of billfishes and the "second anal" in the Recent forms (palaeorhynchids have one continuous anal fin), each with between 6 and 9 rays in istiophorids and 3 in *Xiphias*, to be homologous with the series of finlets (**state 2**). In larval billfishes, one can see on continuous dorsal fin and one continuous anal fin (Fig. 5.34d), which are split into the first and second dorsal and first and second anal later in their development. The first dorsal of billfishes is soft, like the second dorsal of other scombroids. The first dorsal of billfishes also develops ontogenetically in the same way as the second dorsal of, for example, *Thunnus* (Collette *et al.*, 1984 and Potthoff *et al.*, 1986). Just as finlets in *Thunnus* are "caudal extensions" of the

second dorsal fin that are isolated into separate rays, the second dorsal and second anal of the billfishes seem to be separated thus from a continuous soft fin in their ontogeny. Instead of a series of separate brush-like fin rays, however, the separated caudal extensions form a new fin. Evidence that supports this theory can be found in the palaeorhynchids, where, although dorsal and anal fin are long and continuous, one can see in each of them more than one distinct section (Fig. 5.37b) (**state 1**), which to me are the precursors of "new" fins to be separated in later evolutionary stages. This evolution can than be seen repeated in the ontogeny. The number of dorsal or anal finlets in the taxa that possess "true" finlets mostly varies between 4 and 10 (**state 4**) in scombrids and some gempylids (*Gempylus*, *Lepidocybium*, *Thyrsites*, *Thyrsitops* and *Tongaichthys*). All other gempylids that have finlets have between two and three pairs (**state 3**). The absence and presence of finlets is a two-state character in Johnson (1986).

5.2.4.4 Anal fin.

The anal fin is a soft, unpaired fin which is situated in the postero-ventral half of the body. The anus is found anterior to this fin. The anal fin is linked to the vertebral column through a long pterygiophore, which makes close or direct contact with the first haemal spine (Fig. 5.38a), except in istiophorids (Fig. 5.38b). Normally, it is through the first anal pterygiophore that the fin makes contact with the vertebral column (**character 42, state 0**), but, as for example *Coryphaena* and palaeorhynchids show, this is not always the case (see Fig. 5.37b) (**state 1**). In the plesiomorphous condition, the soft fin rays of the anal fin are preceded by one or more short, rigid spines (**character 73, state 0**). Although mostly one, the number of spines varies between one and three. These spines are missing (**state 1**) in the outgroup taxon *Coryphaena* and, within the scombroids, in the trichiurids, *Scomberomorus*, *Acanthocybium*, billfishes, Sardini and Thunnini except *Katsuwonus*. Potthoff *et al.*'s (1986) account of the ontogenetic development is confusing on this point. They mention in the discussion of each scombroid family and tribe, that the first anal pterygiophore bears one or more spines; even in istiophorids, which have clearly only soft rays in their fins. This is because they actually do not make a distinction between anal fin spines or rays (Potthoff *et al.*, 1986, Table 1). In some taxa, the distinction between a first short soft ray and a hard spine are difficult to see (Scomberomorini: Collette & Russo, 1984 and Sardini: Collette & Chao, 1975). These authors therefore have not made the distinction. However, accordinng to my observations, the Sardini do not possess anal fin spines and that within the Scomberomorini, *Scomberomorus* is wanting them. Unfortunately, these observations were made in the collections without realising the importance of it and therefore appropriate drawings or photographs were not made to support these observations. In some taxa, as mentioned before, an

initially continuous anal fin is modified during ontogeny into a first anal and depending on the taxon a second anal and a series of finlets. The number of anal fin rays can be divided into three classes: 7-44 (**character 72, state 0**), as in most of the considered taxa, 45-68 (**state 1**) as in some trichiurids and the palaeorhynchids, and 92-108 (**state 2**) as in some trichiurids.

The configuration of the anal fin pterygiophores in trichiurids is similar to that of their soft dorsal fin: three separate radials present, of which the distal radial is embraced by a soft fin ray.

5.2.4.5 Pectoral girdle.

The pectoral (or shoulder-) girdle is a paired structure, each of the pair consisting of a series of bones: supratemporal, posttemporal, supracleithrum, cleithrum, scapula, coracoid, actinosts and postcleithra (Fig. 5.39). The pectoral girdle is connected to the head and has the pectoral fin articulated to it.

Supratemporal. The supratemporal is a small and thin three-pronged bone, sometimes almost triangular in shape (Fig. 5.39). Each prong bears a sensory canal. The supratemporal is situated ventrolaterally to the anterodorsal process of the posttemporal and makes contact with the pterotic. The supratemporal does not fossilise well, and I have found the significance of its characters for scombroid phylogeny difficult to assess.

Posttemporal. The posttemporal is a flat elliptical bone with a plate-like dorsal surface and two large anterior processes (**character 57, state 0**). These processes, one dorsal and one ventral, connect the rest of the pectoral girdle to the head. The margin of the plate dorsal to the ventral process is often swollen, but in some taxa like *Auxis* it has developed into a sharp-pointed anterior median process (Fig. 5.40a), thus creating a posttemporal that is three- instead of two-pronged (**state 1**). The ventral projection articulates with the dorsal protuberance of the intercalar. The dorsal process is attached to the head through the epiotic, although I have seen it extending into the supratemporal groove. In *Scomberomorus*, although the dorsal process is single, the margin in some specimens seems undulated in a way (Fig. 5.40b), suggesting the tendency to grow into the median anterior process. In some taxa, such as Scombrini, *Acanthocybium* and istiophorids it seems that instead of a real median process, the dorsal process is two-way forked instead. However, there is no real difference with the median process as in *Auxis*, because this also is an axiad lamellar expansion which springs from the dorsal process. Gregory & Conrad (1937) state that percoid fishes have three-pronged posttemporals like istiophorids, but this is not the case in the outgroup taxa that I have chosen.

Supracleithrum. The supracleithrum is an ovoid bone with a small dorsal handle-shaped process (Fig. 5.39). The supracleithrum is overlapped dorsolaterally

by the posttemporal and overlaps the anterior part of the dorsal wing-like extension of the cleithrum (see description of cleithrum). I have not observed a variability in characters of the supracleithrum that are quantifiable and codeable for the phylogenetic analysis.

Cleithrum. The cleithrum is the principal bone of the shoulder girdle (Fig. 5.39). The main body of the cleithrum is crescent-shaped (Figs. 5.39 and 5.41), with an anterodorsal spine and a posteriorly projecting plate just posterior to this spine. The ventral, convex part of the supracleithrum overlaps this dorsal plate. The crescent-shaped main body of the cleithrum consists of an inner and outer shelf, which are joined at the anterior margin of the bone. At the dorsal side of the inner shelf, just ventral to the dorsal plate, the shelf is expanded posteriorly. This expansion may contain a concave, semicircular emargination. The scapula fits perfectly on to that expansion. The only variability that I could observe in cleithra is the degree of curvature, which is not easy to quantify.

Postcleithra. There are two pairs of postcleithra, a pair of dorsal and a pair of ventral postcleithra. The dorsal postcleithrum is connected to the inner surface of the posterodorsal plate of the cleithrum (Fig. 5.42a). Dorsal postcleithra are thin and almost flat, more or less curved (depending on the taxon) bones. The anterior end of the dorsal postcleithrum is tapered, while its posterior end is wider and more or less rounded. Only *Gymnosarda* seems to have a dorsal postcleithrum that is pointed at both sides (Fig. 5.42b). The ventral postcleithrum is a spine-like structure, with a dorsal lamellar expansion. The dorsalmost apex of this bone is connected to the dorsal postcleithrum. The characters of the postcleithra are not included in the phylogenetic analysis, since they do not fossilise well and are difficult to quantify. *Gymnosarda* and other scombroids can be identified by other characters.

Scapula. The scapula is a more or less triangular bone with rounded margins and an eccentric foramen. It connects neatly onto a ridge on the inner shelf of the cleithrum (Fig. 5.39, 5.41). I have discovered no characters that I could quantify for the phylogenetic analysis, in the scapula.

Coracoid. The coracoid is a more or less dagger-shaped bone. Anterodorsally, there is a process which abuts with the posterior margin of the scapula and the posterodorsal part of the inner shelf of the cleithrum (Figs. 5.39, 5.41). Posterodorsally, there is a dorsad-pointing process, with which the fourth radial articulates. The coracoid contains no phylogenetically relevant characters.

Actinosts. The actinosts (also called radials, in for example Collette & Russo, 1984) are small, solid rod-like bones that articulate the pectoral fin to the coracoid and the scapula (Figs. 5.39, 5.31). There are four actinosts (one is missing in Fig. 5.41), of which the most ventral articulates with the coracoid. The actinosts are

rarely found in fossil specimens and identifying characters are hard to discover in them.

5.2.4.6 Pectoral fin.

The pectorals are the most anteriorly placed paired fins. They articulate with the radials and the scapula of the shoulder girdle. In most taxa, the pectoral fin points straight posteriorly or slightly postero-dorsally (Fig. 5.43a). In *Xiphias*, however, these fins rigidly point ventrad (Fig. 5.43b). This being an autapomorphy of *Xiphias* alone, I decided to omit the character from my phylogenetic analysis. The pectoral fin consists soft rays, the first of which is serrated in *Trichiurus gangeticus* Gupta, 1966. Because I found the fin ray counts of the pectoral fin overlapping so much in different groups, I decided not to include this character in the phylogenetic analysis.

5.2.4.7 Pelvic girdle.

The terminology related to the pelvic girdle is taken from Stiassny & Moore, 1992. The pelvic girdle is situated in the anterior half of the body except in *Trichiurus* and *Lepturacanthus*, in which it is missing (**character 75, state 2**). This is also character 39 in Gago (1998). In *Aphanopus*, the pelvic girdle is strongly reduced. In a radiograph I made of BMNH 1961.6.20.1, it comes out so small that its structure is not discernible. I had to turn to Gago (1997, 1998) for this (Fig. 5.44a). Its anterior part is in most cases situated between the cleithra (Fig. 5.44b), posterior to cleithra in *Sphyraena*, *Eupleurogrammus* and *Tentoriceps*. (Fig. 5.44c) and is connected to these through connective tissue. The girdle consists of paired pelvic plates (often called basipterygia). The pelvic girdle makes no bony connection to any part of the skeleton. The pelvic plate can be divided into three sections (Fig. 5.44d): the central part, whose anterior margin lies between the cleithra and the anterior and posterior processes, which seem to originate from the same point anteroventral to the central part. The pelvic fin is inserted on a ridge on the posterior margin of this plate. In the primitive condition, the central part is just a simple bony plate (**state 0**). Maybe one can discern different wings in this plate, but these are not well differentiated (Fig. 5.44e). This condition exists in *Sphyraena*, trichiurids, most gempylids and most outgroups, such as *Trachurus* and *Luvarus*. In "scombriform" gempylids like *Lepidocybium* and *Ruvettus*, outgroups such as *Coryphaena* and *Trachurus*, and all other scombroids, the central part consists of three well-differentiated wings (**state 1**). Stiassny & Moore (1992) identify a maximum of four wings in pelvic plates: internal, external, external ventral and external dorsal. In scombrids, whose pelvic plates I have studied more closely than other taxa, there are three such wings (Fig. 5.44d): the ventral wing is missing. Of all the scombroids with well-differentiated wings, the

scombrids have the most developed ones. Whereas in outgroups like *Trachurus*, trichiurids, gempylids and Scombrini (Fig. 5.44b), the central part of the pelvic plate is simply pointed, the dorsal margin is extended dorsad in a plate-like extension in scombrids other than Scombrini (Fig. 5.44d). Because of this, Collette and co-workers have named the central part in the scombrids the anterodorsal plate (see for example Collette & Chao, 1975 and Collette & Russo, 1984). The posterior processes are basally united into the interpelvic process. In most taxa, this process is shorter than the pelvic fin (**character 59, state 0**), but in *Auxis* and some species of *Scomberomorus*, the interpelvic process is longer than the pelvic fin (Fig. 5.44f) (**state 1**). This is also character 16 in Collette & Russo (1984). In most taxa, the apices of the processes are not united, resulting in a bifid interpelvic process (Fig. 5.44g). In *Benthodesmus*, *Eupleurogrammus*, *Gymnosarda*, *Auxis* and *Gasterochisma*, the interpelvic process is single, with the two posterior processes united over their whole length. (Fig. 5.44f).

5.2.4.8 Pelvic fin.

The pelvic fins are anteroventrally situated, rather close to the head (Figs 5.44b, c). They are connected to the pelvic bones. In *Trichiurus*, *Lepturacanthus*, *Aphanopus* (Nakamura & Parin, 1993 and pers. obs.), *Paradiplospinus*, *Rexichthys*, and *Xiphias* the pelvics are absent. Although *Aphanopus* possesses a reduced pelvic girdle, adult *Aphanopus* do not have pelvic fins. In juveniles, however, they are present as single spines (Nakamura & Parin, 1993). In the plesiomorphous condition, the pelvic fin consists of one hard spine, placed at the lateral side of the fish, and five wide soft rays (Fig. 5.45) (**character 58, state 0**). There are various stages of reduction of this basic bauplan, mainly in trichiurids and gempylids. In *Palaeorhynchus*, there are five well-developed rays, but the spine is not developed (**state 1**). In the outgroup taxon *Luvarus*, in the istiophorids, *Benthodesmus, Gempylus* and some species of *Rexea*, the number of soft rays in the pelvics varies between 1 and 4 (**state 2**). In *Nealotus*, smaller specimens of some species of *Rexea* and most trichiurids, the pelvic fin consists only of the spine (**state 3**). In larger specimens of the *Rexea* species concerned, the pelvic fin is not visible externally, because it is reduced to a subdermal knob (Nakamura & Parin, 1993). In trichiurids, this spine has been modified into a scale-like process (Fig. 5.44e).

5.2.4.9 Caudal fin

General characters. The caudal fin consists of a series of soft lepidotrichia. These can be divided into procurrent and principal rays. The principal rays overlap the hypural elements of the caudal skeleton. The procurrent rays, which precede the

principal rays, do not. The lepidotrichia are paired, the left and right member of each pair adjoined except at their bases, which overlap the hypural plate (Fig. 5.46).

Caudal fin shape. The tail fin (Fig. 5.46a) is forked in all outgroup taxa except for luvarids and in most scombroid taxa (Fig. 5.46a1). In the Scomberomorini there seems to be a tendency towards a development to a more lunar shape of tail (Fig. 5.46a2). Sardini and billfishes have a semilunate tail (Fig. 5.46a3) and Thunnini a lunate tail. (Fig. 5.46a4). The caudal fin shape in scombrids and billfishes is an adaptation to a continuous-cruising mode of swimming. The reduction of the tail fin in gempylids and trichiurids is an adaptation to a mesopelagic and benthopelagic (in deeper waters or close to the bottom of the ocean) lifestyle (Nakamura, 1993c). Because of the difficulty in quantifying the infrataxic variety of this variation, it is not used as a character in the phylogenetic analysis.

Hypurostegy. The lepidotrichia cover only the margins of the caudal complex in most scombroids and the outgroup taxa (Fig. 5.46b) (**character 51, state 0**). In luvarids, the gempylid *Tongaichthys* (Nakamura, 1993b); Nakamura & Parin, 1993); billfishes and scombrids however, the bases of the lepidotrichia are expanded and cover the caudal skeleton almost completely (Fig. 5.46c) (**state 1**). The term to describe this phenomenon was invented by Le Danois & Le Danois (1964) as *hypurostégie*, which has been anglicised into "hypurostegy". Hypurostegy has been used as a character before, in Collette *et al.* (1984, character 14) and Johnson (1986, character 33).

Median lepidotrichia. In most scombroid groups and most of the outgroup taxa, the caudal fin rays have the same width throughout (**character 50, state 0**). In the outgroup taxa *Luvarus* and *Coryphaena*, the billfishes and the scombrids however, a few median lepidotrichia are widened and more widely spaced (Fig. 5.36c) (**state 1**).

Procurrent spur. The procurrent spur is a small inconspicuous outgrowth of the most posterior ventral procurrent caudal fin ray. This outgrowth projects ventrally to overlap the two preceding rays, the first preceding ray being shortened at its base (Fig. 5.46b). It is believed that this structure is an adaptation towards swimming strategies (Johnson, 1975) and occurs in various perciform fishes. According to Johnson (1986, character 15), one of the synapomorphies of the scombroids above the sphyraenids, is the absence of the procurrent spur (**character 56, state 1**). Of all the taxa considered, only *Scombrolabrax* and *Sphyraena* possess this spur (**state 0**). The *Auxis* in Fig. 5.46c clearly does not show a procurrent spur.

5.3 Soft tissue characters

This study involves fossils: about 40% of the data matrix consists of fossil taxa. It is intriguing to know what we can learn from mainly osteological evolution from around the Ypresian until now. Osteological characters play a major role in research into scombroid phylogenetics (Russo, 1983; Collette & Russo, 1984, Gago, 1997 and 1998) However, ignoring all soft-tissue characters would be ignoring evidence that most taxonomists deem important (see for example Kishinouye, 1923; Johnson, 1986). Therefore, a small number of fleshy anatomical characters has to be included. I made a selection of what I view as soft-tissue characters that cannot be ignored; these are presented here. There are characters relating to the head, the trunk, the tail region and the swimbladder. Endothermy-related characters of the myotomes are mentioned separately in a chapter about endothermy (Chapter 4).

5.3.1 Head.

Characters of the head that are of relevance to this study are selected. These are related to the nostrils, tongue and gills.

5.3.1.1 Nostrils.

Normally, two pairs of nostrils are present (**character 24, state 0**). The anterior nostril is usually small and round, the posterior nostril is a long slit (Fig. 5.47a). The posterior nostril is often not immediately visible in live or spirit specimens. Trichiurids have only one pair of nostrils (Fig. 5.47b) (**state 1**), because the posterior external naris is lost during development (Gago, 1997). This character has been used before in Johnson (1986, character 28) and Gago (1997, character 1). This is a very useful character to distinguish them from gempylids that have a more snake-like appearance. This reduction of the nasal apparatus is an adaptation to a more sedentary benthic habit compared to a more active swimming lifestyle of many other scombroids. Billfishes, gempylids and scombrids occur in the upper to the deeper waters of the open ocean (Nakamura, 1989a) and possess two pairs of nostrils. The single nostril in trichiurids functions as both the incurrent and excurrent pore Nakamura (1991a). For constant, fast swimming it is more efficient, from a hydrodynamic point of view, to keep separate external nares for in- and outflow.

5.3.1.2 Tongue.

The basihyal, covered by flesh, tooth patches and cartilage, forms the tongue. The presence or absence of tooth patches on the tongue is discussed in the section of skeletal characters. Besides the possible tooth patches, the tongue is normally

covered by flesh only (**character 17, state 0**). In the Thunnini, except *Allothunnus* (see Nakamura, 1991b), the tongue possesses two lateral cartilaginous crests (**state 1**) (Fig. 5.48). These serve to funnel water over the gills during their continuous fast swimming, thus enhancing the efficiency of respiration Nakamura (1991b). The water jet that is channelled into the gill cavity through this funnel, leaves the individual at the ventral part of the operculum. The pressure this excurrent water jet creates could provide sufficient lift to compensate for the loss of lift caused by the pectoral fins folded close to the body during high-speed swimming. This hypothesis should still be experimentally tested (Collette, 1978).

5.3.1.3 Gills.

As soft-tissue character of the gills I consider the gill filaments. These are soft, filamentous structures that cover the ventral side of the gill arches (Fig. 5.21, 5.49). These are the respiratory organs of the gill arches. The gill filaments of *Acanthocybium* and the billfishes are modified in a remarkable fashion. Firstly, the gill filaments are interconnected by "bridges", formed by cartilaginous outgrowths of the gill filaments. Moreover, the gill filaments are covered by bony tooth plates (**character 32, state 1**). These provide extra support for the latticework of gill filaments with cartilaginous bridges (Fig. 5.49a). These modifications are absent (**state 0**) in other taxa considered. Muir & Kendall (1968) postulated four hypotheses for the function of the cartilaginous latticework. Keeping the function of the tooth plates in mind, the hypothesis that they increase rigidity of the filaments is the most likely. With increased rigidity of large filaments, there is more control over the position of the filaments during fast continuous swimming, as these fishes are known to do. In the Thunnini and *Coryphaena*, gill filaments appear to be interconnected in a similar fashion as in billfishes and *Acanthocybium* (Fig. 5.49b), but in the case of tunas and coryphaenids, the bridges are formed by mucosal epithelium (Muir & Kendall, 1968; Johnson, 1986; pers. obs.) The two modifications of the gill arches discussed here seem co-extensive. The two apomorphous conditions: (bony or cartilaginous) interconnections present, tooth patches present, are only observed together. Johnson (1986), however, treated them as two separate characters (42 and 43). Since these characters are co-extensive and probably adaptations to the same aim (rigidity), I think it is better to treat them as a single character. Collette *et al.* (1984) use the cross-connections of gill filaments as their character 6.

5.3.2 Trunk.

Soft-tissue characters of the trunk that are worth mentioning in this study are those connected to the scale covering, the lateral line and the ventral keel. It seemed

most appropriate to mention the scale covering here, although scales are not really soft body parts.

5.3.2.1 Scale covering.

The most plesiomorphous condition is total covering by large scales (the body is at first glance conspicuously covered by scales, Fig. 5.50a) (**character 79, state 0**). This occurs in outgroups such as *Valamugil* and *Mugil*, the fossils *Blochius*, *Abadzekhia*, *Palimphyes* Agassiz, 1844 and in *Gasterochisma*. Many other scombroids are covered by moderately large scales, (the body is at first glance covered by a finely mazed reticulate network, Fig. 5.50b) (**state 1**). This occurs in the mackerels *Rastrelliger* and *Scombrinus*, in *Grammatorcynus*, gempylids like *Nealotus*, and palaeorhynchids. Most scombroids are covered by small scales, which are difficult to see with the naked eye (**state 2**). The Sardini, Thunnini and †*Palaeothunnus* possess an anterior corselet of moderately large scales. This corselet starts immediately posterior of the head, expands around the bases of the pelvic and pectoral fins and the anterior part of the first dorsal fin, and expands posteriorly for some length ventral of the first dorsal fin. The rest of the body is (almost) completely naked (Fig. 5.50c) (**state 3**). In *Scomber* and *Rastrelliger* the region immediately posterior to the head is covered by scales that are larger than those covering other parts of the body. However, these are not real corselet scales, because they are not remarkably thickened and not much larger than the other scales. Moreover, a corselet always seem to go together with an otherwise almost naked body, while *Scomber* and *Rastrelliger* are still entirely covered by scales. The presence or absence of the anterior corselet is Collette *et al.*'s (1984) character 22. A specimen of a tuna-like fish, formerly known as *Thynnus lanceolatus* (Agassiz, 1835), and to be re-described and renamed (§ 7.3), possesses an anteroventral corselet (Fig. 5.50d) (**state 4**), in which a small patch of large scales surrounds the area around the pelvic fins. It is not clear where the anterior margin of this corselet lies. In case of an anteroventral corselet the rest of the body is also naked. A few fossil taxa are only known from the head and a tiny preserved section of the trunk. The opercular bones and the anterior part of the trunk of these specimens are (partially) covered by moderately large scales. Because the whole body is not preserved, it is not clear whether they possess a corselet like the Sardini and Thunnini or whether they are completely covered by scales. The taxa in question are *Scombramphodon*, *Sphyraenodus*, *Woodwardella* and a species previously known as *Scombrinus macropomus*. The skin of *Ruvettus* is rough and feels like coarse sandpaper. Its small scales are interspersed with spiny rigid tubercles (Fig. 5.50e). *Lepidocybium* is entirely covered by small scales which are each surrounded by a network of rigid tubules (Fig. 5.50f). *Thyrsitoides*, *Neoepinnula* and *Tongaichthys* are other gempylids entirely covered by small

scales, but without interspersed tubercles. *Rexea* is either completely or partially covered by scales, or naked (**state 5**), depending on the species. Other gempylids than the ones mentioned above are naked. Istiophorids are also covered with small scales. *Xiphias* is naked, as are the Scomberomorini and Trichiurids. In smaller specimens (BMNH 1939.5.2.22-24 and/or BMNH 1862.11.23.6-7) of *Trichiurus* I have seen large (as compared to the size of the specimens) scales. I am unaware of the presence or the size of scales on juvenile specimens of *Trichiurus* but it seems unlikely that these scales actually belong to these specimens, since I have seen no other trichiurid, at any stage of its development, with scales. The specimens in question must be contaminated by scales of individuals of other taxa, which then stuck to these *Trichiurus* specimens.

5.3.2.2. Lateral line.

The lateral line is a series of sensory organs enclosed in tubular scales, along the sides of the body. Most of the taxa considered here have a single straight lateral line. The line may be more or less straight with only a slight curve (Fig. 5.51a) undulated antero-dorsad (Fig. 5.51b). *Makaira mazara* (Jordan & Snyder, 1901) has a lateral line system with loops and *Makaira nigricans* Lacépède, 1802 has a reticulate lateral line system (Fig. 5.51c, d). The gempylids *Epinnula*, *Neoepinnula*, *Gempylus*, *Rexichthys*, *Thyrsitoides* and *Rexea* have double lateral lines (Fig. 5.51e), as does *Grammatorcynus*. *Lepidocybium* has a wavy single lateral line (Fig. 5.51f). In *Xiphias* the lateral line is completely lacking. These lateral line characters are not used in the phylogenetic analysis, because they can hardly be found in fossil specimens and the taxa in question can be identified by other characters. However, lateral lines provide indispensable field-identification characters.

5.3.3 Tail region.

Two soft-tissue characters of the tail region are relevant: the mid-lateral keels and the smaller lateral keels (Figs. 5.52a-e).

5.3.3.1 Mid-lateral keel.

The presence of a small fleshy lateral keel on the caudal peduncle is thought to be an adaptation towards an improved swimming performance. The water-stream along the edges of this keel can contribute in a hydrodynamic lift (compare to wings of aeroplanes) and enhance a smooth passage through the water. The gempylid *Lepidocybium* has a weakly developed mid-lateral keel (**character 47, state 1**), just as the Scomberomorini (Fig. 5.52a). This keel is only slightly elevated from the surrounding tail stem. The Sardini, Thunnini and *Xiphias* have a well-developed mid-lateral keel (Figs. 5.52b, c) (**state 2**), which sharply differs

from the less well developed keel in some other groups by being clearly elevated from the surrounding tail stem and clearly bulging laterally. In the Sardini and Thunnini, this fleshy keel is supported by a bony keel on the caudal end of the vertebral column (§ 5.2.2.6). Other scombroids and outgroup taxa lack this keel (**state 0**). The absence or presence of the mid-lateral keel (as a two-state character) has been used in the phylogenetic analyses of Collette *et al.* (1984, character 11) and Johnson (1986, character 38).

5.3.3.2 Lateral caudal keels.

In some taxa, two small fleshy keels can be found at both the left and the right side of the caudal peduncle (**character 48, state 1**). One keel is found near the dorsal, another near the ventral lobe of the caudal fin (Fig. 5.52a, b, e). Fierstine & Walters (1968) suggest a function of these keels to promote hydrodynamic efficiency. On both sides of the tail, the pair of keels converge posteriorly. Thus, it is thought that this structure accelerates water flow past the midline of the tail and reduces water turbulence at the tips of the fin. Nakamura & Parin (1993) call them the supplementary caudal keels. This term would be correct if these small keels add functionality to the larger mid-lateral keel. However, as Fierstine & Walters (1968) suggest, this is not the case. Moreover, Nakamura (1993b) shows that *Tongaichthys* and *Thyrsitoides* already possess small keel-like processes (Fig. 5.52d). In the Scombrini and *Gasterochisma*, probably the more plesiomorphous scombrids, these lateral keels are present, while the central keel is absent (Fig.5.52e). It seems thus, that the lateral keels appear in more plesiomorphous groups, while the mid-lateral keel is absent. In the vast majority of cases, the mid-lateral keel is only present if there are also lateral keels. The only exception seems to be *Xiphias*, which has a mid-lateral keel, but no lateral keels (Fig. 5.52c; 5.53a). It thus seems incorrect to suppose that these small keels add supplementary function to the larger mid-lateral keel. I therefore maintain the term lateral keels for these structures. Istiophorids also possess lateral keels, but lack a mid-lateral one. *Lepidocybium*, Scomberomorini, Sardini and Thunnini all possess lateral keels together with a mid-lateral keel. Other groups than those mentioned above lack lateral keels (**state 0**). This character has been employed in phylogenetic analyses before: Collette *et al.* (1984, character 12), Johnson (1986, character 14).

5.3.4 Swimbladder.

Most teleosts possess an air-filled sac in their visceral cavity. It is known under various names, such as air bladder and gas bladder. I use the name swimbladder for this structure. This air-filled bladder makes the density of the fish about equal to the surrounding water (Alexander, 1967). Many scombroids indeed possess these bladders. However, the swimbladder is not a necessity for life, and

some taxa can well survive without it. All Scombrini except *Scomber scombrus* possess a swimbladder (Magnuson, 1972; Matsui, 1967). Within the Scomberomorini, *Scomberomorus* does not possess a swimbladder (**character 78, state 2**), but it is present in *Grammatorcynus* and *Acanthocybium*. In Sardini, *Gymnosarda* is the only taxon with a swimbladder. In the Thunnini the presence or absence of a swimbladder is a very variable character. All billfishes possess a swimbladder (data from Magnuson, 1972). The presence or absence of a swimbladder is character 18 in Collette & Russo (1984). Some species such as *Scomber scombrus*, *Sarda chiliensis*, *Katsuwonus pelamis*, *Euthynnus affinis* and *Thunnus albacares* (Bonaterre, 1788) swim continuously (see Magnuson, 1970). Continuous swimming overcomes negative buoyancy due to the lack of the swimbladder. While swimming continuously, adaptations as (long) pectoral fins which are expanded laterally during swimming and the caudal keels provide some extra lift.

In most fishes, the swimbladder is a sac consisting of one single compartment (Fig. 5.53a) (**state 0**). In Istiophoridae, the swimbladder consists of many small bubble-like chambers (Fig. 5.53b) (**state 1**).

I have not dissected specimens of gempylids and trichiurids to examine the presence, and nature of swimbladders. I have been unable to find data about possible swimbladders in these fishes. I assume, that for their benthopelagic and mesopelagic lifestyles they do not need a swimbladder. If they possess one none the less, it is likely to be strongly reduced. Hopefully, the dissection of fresh specimens will solve this question.

5.4 Larval developmental characters

There are just two characters of larval-development employed in this phylogenetic analysis. As expected, both of them are missing entries in all fossil taxa used. One larval character concerns the morphology of the beak, the other the development of peculiar synapomorphies in certain scombroid taxa that are grouped as one character.

5.4.1 Beak morphology.

Collette *et al.* (1984, character 5) and Johnson (1986, character 41) mentioned some unique developments in the snout region of scombroids, which are described by Johnson (1986) in detail. In the scombrids above *Grammatorcynus* (*sensu* Johnson, 1986), not only is the larval beak of these taxa generally longer than in percoids and other taxa, but the structure of the elements is also different. Johnson (1986) states that the two anterior processes of the premaxilla are not separate. However, the figure that Johnson provides with the description of that character

(see Fig. 5.54a, b) seems to show two distinct anterior premaxillary processes. It is not clear from this figure, however, if these are really two separate processes or if these two "processes" are connected by a thin, lamellar bone which is obscured in Johnson's original photograph. Although I will follow Johnson's observations here, I suggest further examination of specimens to confirm Johnson's (1986) statements on this matter. Johnson (1986) also notes that the rostral cartilage (a block of cartilage between the upper jaw and the neurocranium) has a long horizontal, rather than a long vertical axis. *Acanthocybium*, *Scomberomorus* and the billfishes have a further elongated larval beak, which is horizontal and protrudes like a bird's beak (Fig. 5.54b) (**character 16, state 1**). This is an argument Johnson (1986) uses in favour of his *Scomberomorus-Acanthocybium*-billfish clade. What is clear from my own observations is that *Istiophorus* does have such an elongated larval beak. *Acanthocybium* also has an elongated beak (Collette *et al.*, 1984, Fig. 327). The larval beak of a *Scomberomorus sp.* of 25 mm FL (BMNH 1935.4.24.25) is not elongated (**state 0**), as is the beak of a 5.0 mm *Scomberomorus cavalla* (Cuvier, 1829) in Collette *et al.* (1984) (see Fig. 5.55a). The only explanation for this that I can think of, is that this trait shows interspecific variation within *Scomberomorus*: some species will have elongated larval beaks, some not. Because I have not personally seen larval *Scomberomorus* and because the literature provides conflicting data, this trait is coded with a question mark in the data matrix. *Gymnosarda* also has an elongated larval beak (Collette *et al.* 1984, Fig. 327), but its internal structure is not known.

5.4.2 Combined larval apomorphies

Johnson (1986) notes a peculiar combination of traits which he grouped as one single character. Using Johnson's (1986) sequence, these traits are absent in outgroups and most scombroids (Johnson's character state 18) (my **character 80, state 0**), present in gempylids and trichiurids (Johnson's state 18), the last of which are characterised by a further derivation of these apomorphies (Johnson's state 18'). The apomorphies in question are the following. The pelvics are precocious and the pelvic fin spines (except in *Thyrsitops*) are serrated. Other apomorphies are a relatively deep and steeply graduated first dorsal fin with serrated spines, and a long, serrate spine at the caudal margin of the preoperculum (compare Figs. 5.55a and b) (**state 2**). Because the pelvics in trichiurid larvae are somewhat smaller than those in gempylids, Johnson (1986) concludes that trichiurid larvae are more derived than those of gempylids. I think however, that this argument does not follow. Trichiurid pelvics might have developed early (if at all), but are underdeveloped compared to those of gempylids. The serrated first dorsal fin spines of trichiurid larvae are relatively less long than those of gempylids. Also, trichiurids do not possess a long preopercular spine (but see larva of

Benthodesmus in Collette *et al.*, 1984, Fig. 320, but this spine is not serrated) (Fig. 5.55c). Trichiurids may have an advanced larval morphology (**state 1**) compared to scombrids, but it is plesiomorphous compared to the condition in gempylids. Although Collette *et al.* describe the gempylid and trichiurid larvae in some detail where possible, they did not sure these combined larval apomorphies as phylogenetic characters. Gago (1997) has separated these larval apomorphies, in his characters 2, 13, 16, 19 and 21. I, however, follow Johnson (1986) who perceived that these apomorphies are co-extensive.

CHAPTER 6: STUDY OF RECENT TAXA

6.1 Material and methods

6.1.1 Material

A short introductory study on fish osteology was first carried out, preparing fish bought at the fishmonger's to study the skeletons. The osteological data of Recent fish studied will be processed in data matrices in the same way as their fossil counterparts.

On the first "field trip" to the fish store two salmon heads were bought for a general reference and testing of methods to prepare fish skeletons. The two salmon heads were nicknamed "Enid" and "Jeffrey". For a first study of scombroids, two specimens of *Auxis* Cuvier, 1829 are examined, nicknamed "Jude" and "Eleanor" (collection numbers respectively KAM 2 and 3, KAM indicating my own private collection) and three specimens of *Scomber*, nicknamed "Curly", "Larry" and "Moe" (collection numbers respectively: KAM 4, 5 and 6). The *Auxis* specimens were sold to me as "bonitos", which I accepted as such, having a poor knowledge of scombroids then. Osteological study of the specimens revealed they are in fact *Auxis*. One specimen of *Thunnus alalunga* nicknamed "Brenda", collection number KAM 1, has also been examined.

Other specimens were studied at the National Museum of Natural History (Smithsonian Institution, Washington DC) and the Natural History Museum in London. The specimens I have studied have been prepared in a variety of ways. I have studied skeletal specimens, dried complete specimens, stuffed fish, spirit specimens, cleared and stained specimens and a few fresh fish (in my own collection).

6.1.3 Methods

The specimens I obtained from the fishmongers were preparated using a fish steamer, in which they were steamed/boiled long enough to be easily defleshed afterwards. Subsequently, the skulls, or entire skeletons were cleaned up and where necessary, repaired if disarticulated. These bony and cartilaginous remains were treated in formalin to ensure that all parts kept their original sizes and shapes. An earlier plan to deflesh fish specimens in the BMNH using dermestid beetles was abandoned, since it was thought the beetles do not like scombroid flesh (Collette, pers. comm., 1998). However, according to T.N. Gill (pers. comm., 1999) of the Natural History Museum in London, if the scombroid specimens are treated to remove the body oils and fats before feeding them to the beetles, the results should be satisfactory. I hoped to pursue this technique in the future.

I have radiographed a few spirit specimens in the Natural History Museum in London. The specimens that have been radiographed are indicated as such in the specimen list (Appendix 1). Studying radiographs was a very useful way to study the osteology without damaging the specimens. The association of dorsal fin elements to neural spines (§ 5.2.4.3), the exact position of the pelvic girdle in relation to the rest of the skeleton, fin ray counts, and the possession of predorsal bones were aspects of the study that could be either better counted or better understood from the radiographs.

A few small spirit specimens in the Natural History Museum in London have been subject to a clearing and staining technique, by T.N. Gill of the museum, on my behalf. The aim was to clear the soft tissues, stain the bones with alizarin red stain to a pinkish red colour, and the cartilage blue with alcian blue stain. The method of clearing and staining was based on Potthoff (1984). Cleared and stained specimens, whether found as such in the London collection, or cleared and stained on my behalf, are indicated as such in the specimens list (Appendix 1). Studying cleared and stained specimens offers the same advantages as studying radiographs. Moreover, bone and cartilage tissue can now be easily identified. The structure and configuration of the various bone and cartilaginous elements of the gill arches can now be studied very well, and in their three-dimensional nature. If various specimens of the same taxon exist, the risk can be taken to take apart the cleared and stained specimens, to study some bone elements better.

CHAPTER 7: (RE)DESCRIPTIONS OF FOSSIL TAXA

7.1 Introduction

The aim of studying fossil scombroids is twofold. On the one hand, they are part of the systematic study of scombroids as a whole. On the other hand, the opportunity is seized to revise these taxa in their own right.

The fossil taxa have been subject, just as their Recent relatives, to a system of recording certain of their characteristics in coded form in a data matrix. The fossils are thus made part of a phylogenetic analysis, in the hope that an agreement can be met between the conflicting hypotheses on their phylogenetic relationships. Although I realise the shortcomings of fossils compared to Recent taxa in such analyses (see § 3.2), these shortcomings are dealt with using techniques such as safe taxa deletion (§§ 8.1, 8.2).

Many descriptions of fossil scombroids have been made a long time ago (e.g. Casier, 1966; Bannikov, 1985). It was felt that it was time to update the existing monographs, incorporating taxa described after Casier's and Bannikov's monographs, to describe undescribed specimens and/or taxa, and to revise nomenclature. If different sources mentioning fossil scombroids are compared, the inconsistency in nomenclature and systematics (made worse by unclear systematics in Recent forms) is staggering.

7.2 Material

The fossil material referred to in this thesis is stored in the collection of a few institutions. Because of the large number of scombroid fossils known and stored world-wide and the time restriction of a PhD project, I had to limit the amount of material for study. It seemed obvious to start in England, where I was based for my thesis work. The Natural History Museum (London) contains a large collection of London Clay scombroids, which form the bulk of the scombroid material in that institute. Monographs on these are given in Woodward (1901) and Casier (1966). Another obvious place to look for scombroid fossils was the Paleontological Institute in Moscow. In the past, many scombroid fish were collected in the former USSR. Monographic descriptions of these were given by Danil'chenko (1960) and Bannikov (1985). My research visit to the Smithsonian in Washington DC was mainly to benefit from the large collection of Recent scombroids and the experience of renowned workers such as Collette, Johnson and Tyler. However, most of their interesting collection of scombroid fossils has been studied during the time I had left. Fossils from the collection in Glasgow were taken on loan

during a short stay there for a conference. Some specimens in the institutes I visited have remained unstudied. There are more scombroid fossils known from institutes in, amongst others, Belgium, Japan and Italy.

Bannikov (1993a) transferred *Isurichthys* Woodward, 1901 from the scombroids (family Scombridae, *cf.* Agassiz, 1833-44; Wettstein, 1886, as *Isurus* Agassiz, 1844; Woodward, 1901, as *Isurichthys*) to the perciform family Ariommidae. Initially, I followed Bannikov and thus decided to ignore *Isurichthys* in this study. A careful look at Bannikov (1993a) however, leaves the classification of *Isurichthys* as an ariommid in doubt. Bannikov (1993a) based his classification on characters such as the closeness of the two dorsal fins and the number of vertebrae (±30). However, none of the (combination of) characters thus used by Bannikov are unique to ariommids. In other words, Bannikov (1993a) offers no synapomorphies that justify a removal of *Isurichthys* from the scombroids. Not having studied any specimens of *Isurichthys* myself, I am not able to comment on their systematic status.

Institution abbreviations

BMNH	Natural History Museum, London
GLAHM	University of Glasgow, Hunterian Museum, Glasgow
PIN	Russian Academy of Sciences, Paleontological Institute, Moscow
USNM	Natural History Museum, Smithsonian Institution, Washington DC

7.3 Systematic palaeontology

Below, a systematic account of the fossil taxa is presented. First, the scombroids are described. After the descriptions of scombroids I describe specimens that have been described or labelled as scombroid but have turned out to be something else.

The systematics applied in this section differs somewhat from previously used ones and also somewhat from that used in previous chapters of the thesis. The systematic divisions employed here are based on the results of the phylogenetic analysis (Chapter 8).

Before this section was written, the systematic status of the supposed fossil billfish belonging to the Palaeorhynchidae and Blochiidae *sensu* Schultz (1987) was not clear. It was doubtful whether these are scombroids at all (e.g. Bonde, pers. comm., 1997). In this Systematic Palaeontology, the palaeorhynchins and *Blochius* have been included within the scombroids. It must be mentioned at this point that a thorough large-scale revision of *Blochius* has recently started. Insights presented by a relatively superficial study of *Blochius*, presented here, will be possibly overturned by that study.

Most of the descriptions of previously known taxa are kept concise, concentrating on the difference between the original description and my own observations. I acknowledge that many of the descriptions of Russian taxa, given here, are still insufficient for many readers, because my descriptions and remarks are concise, and I refer for more detail to descriptions that are available only in Russian (Bannikov, 1985 and 1989; Danil'chenko, 1962 and 1980). I feel that, within a project like this, translations of descriptions in these papers should have been part of the systematic palaeontology. However, it was felt too, that within the time limits of a PhD project it was not possible to pursue this. I intend to proceed to incorporate these translations within future published descriptions. New taxa, named here, are obviously given an as detailed as possible description.

Russian stratigraphical terms, like Svita (literal translation: Suite) and Horizon are maintained in the Systematic Palaeontology section and the specimen list (Appendix 1), rather than translating them to "Western equivalents" such as Formation, as is sometimes done (e.g. in Patterson, 1993). Holland (1983) makes it clear that Russian stratigraphy works with different definitions and with different methodologies. Hence, there is no exact "Western equivalent" for the respective Russian stratigraphical terms.

Fossil specimens of *Sphyraena* have been studied (see Appendix 1), but are not described below. In the provisional cladistic analysis (Chapter 8), *Sphyraena* appears to be more parsimoniously placed in the outgroup rather than the ingroup of scombroids.

Suborder **SCOMBROIDEI** Bleeker, 1859

Family **TRICHIURIDAE** *sensu novo*

Subfamily **TRICHIURINAE** Rafinesque-Schmaltz, 1815

Genus *Casierichthys* gen. nov.

Etymology. The genus is named in honour of the late Edgard Casier, expert on Tertiary fishes, amongst others, scombroids.

Diagnosis. Concave suboperculum, teeth labio-lingually widened and abruptly tapered at apex.

Type species. Only one species known, described below

Species composition. The type species only.

Casierichthys morsensis sp. nov. (Figs. 7.1, 7.2)

Etymology. The only specimen known so far was found on the island of Mors, Denmark.

Diagnosis. As for genus.

Holotype Two counterparts of skull: BMNH P23994 and P23995 (labelled as unidentified teleost), Skarrehage Pit, Island of Mors, Denmark, Early Eocene: Ypresian (Mo-Clay Formation).

Description. Only fragmented skull material and some parts of shoulder girdle known. Premaxilla-maxilla complex tightly bound, non-protrusible. Premaxilla with cavity, possibly empty socket of shed fang, but serial teeth missing. Palatine with many empty small, circular tooth sockets. Hind margin of palatine near anterior bifurcation of parasphenoid. Dentary long, elongate, protruding upper jaw complex and tapering to very slender anterior end. Dentary teeth not very large, but stout and sharp. Anterior teeth smaller, conical and curved in posteriorly. Distal teeth larger, wider and acutely tapered near apex. Angular short and triangular, apex directed anteriorly. Quadrate triangular, rather large, short except for the long, posteroventral projection. Left frontal poorly preserved, right frontal missing. Basioccipital widened posteriorly and bifurcated anteriorly. Long and narrow parasphenoid inserted into basioccipital. Parasphenoid bifurcates anteriorly before halfway its length. Hyomandibular damaged, seemingly small with relatively large articulating process (which would have articulated with pterotic). Operculum large, almost as long as dentary, fringed and widening distally. Suboperculum small and narrow, about 0.75 of operculum length, its posteroventral margin slightly concave. Interoperculum damaged. Preoperculum long and slender, consisting of two wings, at an angle of approximately 120°. Ventral wing about 1.5 times length of dorsal wing. Branched preopercular sensory canal well preserved. Entopterygoid attached to hyomandibular: long lamellar bone, almost as long as palatine, with convex inner margin. Entopterygoid and metapterygoid missing. Posttemporal fairly small, with two anterior articulary processes, forming angle of about 58° to each other. Two processes of different length. It is assumed that longest of two processes is median process (which attaches to epiotic), as always seems to be the case in Scombroids. Posteriorly, posttemporal attached to supracleithrum, which is flat and thin, apically slightly narrower.

Remarks. These specimens, counterparts of the same individual, clearly belong to a trichiurin. The premaxilla seems to be tightly bound to the maxilla, which is a scombroid synapomorphy. The lower jaw would have protruded the upper jaw in life, which is a synapomorphy of trichiurins+gempylins. Within the scombroids, only trichiurins have fimbriated opercular bones and all trichiurins have toothed palatines. All these conditions are present in the fossil (Fig. 7.2a). The ventral margin of the suboperculum is concave, therefore this specimen belongs to the subfamily Trichiurinae as defined by Tucker (1956). According to Tucker's definition, Recent trichiurin genera are *Trichiurus* and *Lepturacanthus*. This fossil cannot be identified as belonging to either of these genera. The dentition seems to

be different from those of other trichiurins. Tooth marks in specimen P23995 (Fig. 7.2b) reveal teeth that are shorter and taper more abruptly at the apex. The empty socket of a premaxilla fang (Fig. 7.2a) is preserved, but there are no traces of serial premaxillary teeth. This predator (as trichiurins are), must have had many sharp teeth in the upper jaws. The lower jaws clearly do. Also, near the lower jaw are traces of upper jaw teeth, corresponding with those of the lower jaw (difficult to reproduce in the figures). The shape of the operculum also indicates that *Casierichthys* is not referable to an already described trichiurin. It differs from the shape of the operculum of both *Trichiurus* and *Lepturacanthus*, both in which the operculum tends to narrow distally. In *Casierichthys* however, the operculum becomes broader distally. Since it is not possible to assign *Casierichthys* to a Recent trichiurin genus, is it possible then to assign it to a previously described fossil one? Except for *Trichiurus* there are no known trichiurin fossils. The systematic status of the fossil genus *Eutrichiurides* cannot be established for lack of phylogenetically relevant characters (see description of *Eutrichiurides*, below), although it has previously been thought to be a trichiurin (Arambourg, 1952; Casier, 1944, 1946 and 1966; Leriche, 1910). The teeth of *Eutrichiurides* are rather large (see below). The teeth of *Casierichthys* are considerably smaller. Thus, BMNH P23994 and P23995 cannot be assigned to *Eutrichiurides* and a new fossil monospecific genus is established.

Genus ***Trichiurus*** Linnaeus, 1758

Trichiurus Linnaeus, 1758: 246

Enchelyopus Bleeker (1862): 109 (*non* Gronovius, 1763).

Lepturus Gill (1864): 225 (*Lepturus* Artedi, 1738 unavailable; *non* Moehring, 1758).

Clupea Forsskål, 1775: 72 (*non* Linnaeus, 1758).

Lepturacanthus Dutt, 1967: 756 (*non* Fowler, 1905).

Diagnosis. Fossil *Trichiurus* are known from teeth only. Characteristic are the curved fangs, which are curved like an "S" (Fig. 7.3) and whose tips may or may not be barbed, depending on the species. I have not seen any *Trichiurus* teeth that can be specifically identified.

Trichiurus oshosunensis White (1926) is said to be found in Lutetian of Nigeria (White, 1926), the Ypresian of Congo-Kinshasa (Dartevelle & Casier, 1949) and the Early Eocene of Tunisia (Arambourg, 1952). I have studied Nigerian specimens (BMNH P24270-9), which are similar to White's (1926) description, according to which they "cannot be confused with other species". However, neither this description nor the studied specimens seem to contain any specific apomorphies.

Trichiurus sp. (Fig. 7.3)

Diagnosis. As for genus.

Referred material USNM 291178, South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Miocene (Fish Stratigraphic Column, Pungo River Formation); BMNH P15599-601, Noil Tobé, Timor, Eocene; BMNH P26354 and P26357-9, Bracklesham Bay, Sussex, England, Middle Eocene (Bracklesham Beds), BMNH P24270-9, Oshosun, South Nigeria, Lutetian.

Remarks. It is clear that these teeth belong to *Trichiurus*, but there are no diagnostic characters to identify the species. Some of the specimens concerned here have a specific epithet attached to them (see Appendix 1), but I do not know on what basis these identifications are made. Since the *Trichiurus* teeth do not possess any specific characters that I know of, I have decided to categorise them all as *Trichiurus* sp. Two of these specimens are pictured in Fig. 7.3.

Genus *Anenchelum* De Blainville, 1818

Anenchelum De Blainville, 1818: 314.

Lepidopides Heckel, 1850: 239.

Lepidopus Wettstein (1886): 38 (*non* Goüan, 1770).

Diagnosis. Caudal fin present (Fig. 7.4). Long continuous dorsal fin with clear discernible anterior portion of 30-35 hard spines. Differs from *Lepidopus* through clearer differentiation between hard and soft portion of dorsal fin, more anterior fin spines, an incomplete association of soft dorsal pterygiophores with neural spines (see below) and the absence of a cranial crest. Differs from the Aphanopinae (*Benthodesmus* and *Aphanopus*) by a more posteriorly (behind base of pectoral fin) placed pelvic and the first and second anal fin elements close together.

Remarks. This genus was originally known as *Anenchelum*. It shows a strong resemblance to *Lepidopus* (see Agassiz, 1833-44). Wettstein (1886) thought that differences between *Lepidopus* and *Anenchelum* were very light-weight and mostly artefacts of fossilisation. All authors seem to have followed Wettstein in this (e.g. Woodward, 1901; Arambourg (1927); Danil'chenko, 1960, 1962 and 1980; Sorbini, 1987). Bannikov & Parin (1995) revised the characteristics that define *Anenchelum* and found that there are differences between *Anenchelum* and *Lepidopus* which go beyond artefacts of fossilisation. *Anenchelum* posseses characteristics of both the trichiurid subfamilies Lepidopinae and Aphanopinae, as defined by established by Tucker (1956), but does not fit the diagnoses for either. The loose association of the soft fin pterygiophores with the neural spines (a plesiomorphy, see § 5.2.4.3) is, for example, an aphanopin character state, as is the

number of first dorsal fin elements (30-35), which is more similar to the situation in aphanopins (33-46) than it is in lepidopins (eight in *Lepidopus*). In *Lepidopus* the pterygiophores have a complete association with the neural spines, which is the apomorphous character state. It is one of the most easily discernible characters which indicate that *Anenchelum* is not a *Lepidopus*. However, care must be taken in interpreting this character from fossils. During the process of fossilisation, the specimen may be distorted or certain parts of the skeleton may be moved from their natural position. Hence, pterygiophores which are loosely associated with neural spines might have been well associated with these spines in life. Some specimens labelled *Anenchelum* can therefore, without additional information, not surely be labelled as such. In specimens where the dorsal fins seem to be in their natural position, a positive identification can be made. Although, especially in the context of fossils, a character like the association of pterygiophores to spines does not sound robust or convincing, my own radiographs of Recent trichiurins have proven the usefulness of this character (see Fig. 5.36).

Species compostion. Only fossil species are known. They are found from the Eocene to the Early Miocene in Spain, Switzerland, the Caucasus region, and possibly Hungary (Bannikov & Parin, 1995). Bannikov & Parin (1995) do not mention *Anenchelum brevicauda* Vom Rath, 1859. Wettstein (1886) convincingly identifies it as a separate species (as *Lepidopus brevicauda*). Bannikov & Parin (1995) found that *Lepidopus eocaenicus* Danil'chenko (1962) should be transferred to *Anenchelum*. I have studied the holotype of *L. eocaenicus*, which is the head and a few precaudal vertebrae. I find that in that specimen, not enough details are preserved to assign it to either *Anenchelum*, *Lepidopus* or another trichiurin. Below, descriptions of *Anenchelum paucivertebrale* Bannikov & Parin, 1995 and *Anenchelum glarisianum* De Blainville, 1818 follow.

Anenchelum glarisianum De Blainville, 1818 (Fig. 7.4).

Anenchelum glarisianum De Blainville, 1818: 314. Type loc. Canton Glarus, Switzerland, Oligocene.

Anenchelum latum Agassiz, 1834: 302 (*nomen nudum*). Type loc. *ibid.*

Anenchelum isopleurum Agassiz, *l.c.*: 302 (*nomen nudum*). Type loc. *ibid.*

Anenchelum heteropleurum Agassiz, *l.c.* 132 (*nomen nudum*). Type loc. *ibid.*

Anenchelum isopleurum Agassiz, 1833-44:71, pl. 37, fig. 3.

Anenchelum dorsale Agassiz, *l.c.*: 72, pl. 37, fig. 4.

Anenchelum heteropleurum Agassiz, *l.c.*: 73, pl. 37*a*, fig. 3.

Anenchelum latum Agassiz, *l.c.*: 74, pl. 36.

Anenchelum breviceps Giebel, 1847: 665. Type loc. *ibid.*

Lepidopides leptospondylus Heckel, 1850: 240, Plate XXII. Type loc. Galicia, Oligocene.

Lepidopides dubius Heckel, *l.c.*: 241. Type loc *ibid.*

Lepidopides brevisponylus Heckel, *l.c.*: 241. Type loc. *ibid.*

Lepidopus carpathicus Kramberger-Gorjanovic´, 1879: 57, Plate XVI, fig. 1. Type loc. *ibid.*

Lepidopus leptospondylus Kramberger-Gorjanović, *l.c.*: 57. Type loc. *ibid.*

Lepidopus glaronensis Wettstein, 1886: 42, pl. V, figs. 1, 3, 5, 9, 10; pl. VI, figs. 1,3,5-8. Type loc. Canton Glarus, Switzerland, Oligocene.

Lepidopus glarisianus Woodward, 1901: 477. Type loc. *ibid.*

Lepidopus angustus Danil'chenko, 1980: 151, pl. VII, figs. 1, 2. Type loc. River Belaya, Russia, Oligocene.

Anenchelum angustum Bannikov & Parin, 1995: 184.

Diagnosis. Twelve or thirteen Pairs of teeth in both upper and lower jaw. 106-116 Vertebrae. Length up to 2 m.

Referred specimens. BMNH 41807, 41808, 41812, P442 (**Holotype** of *A. isopleurum*), P451, P3994, P10856, P1711, P40132, P65193; Engi, Canton Glarus, Switzerland, Early Oligocene: Rupelian (Glarnerschiefers). PIN 1413-88, 1413-93, 1413-94 (**holotype** of *Lepidopus angustus*); 3363-17, **Paratype** of *Lepidopus angustus*; 3363-143 and 3363-144, river Belaya, Caucasus, Russia, Early Oligocene: Rupelian (Khadum deposits).

Description. A detailed recent description of this species is given in Dani'chenko (1960). Additional information is given here. Elongated, snake-like fish (fig. 7.4a). Small specimens have been measured to be 257-316 mm long (forklength). A specimen consisting of 42 caudal vertebrae (BMNH 41808) and the caudal region (Fig. 7.4b) is 351 mm long (forklength). A specimen consisting of 33 precaudal and caudal vertebrae (BMNH P65193) is 248 mm long. Specimens up to 2 m are known (Danil'chenko, 1966). Ceratohyal without ventral projections. Ventral margin of subopercului convex. Pectoral fin with 11 rays. Pelvic plate bearing reduced pelvic fin, possibly consisting of spine without soft rays (according to Danil'chenko, scale reduced to small scale-like process). Vertebral column with 106-116 vertebrae (105-110 *sensu* Danil'chenko), 34-39 of which are precaudal (33-37 *sensu* Danil'chenko). Caudal skeleton with two epurals. Hypural plate split in dorsal and ventral plate. Fifth hypural and parhypural autogenous. Thirty caudal fin rays. No hypurostegy. Procurrent spur absent. One continuous dorsal fin, consisting of anterior part of 30-35 hard spines and remainder with 70-81 soft rays. Danil'chenko did not take the division betwween the soft and rigid part of the dorsal fin into account and counted a total of 98-104 dorsal fin elements. First pterygiophore inserted in second interneural space. Anal fin with I spine and 62-64 soft rays. Danil'chenko (1960) states that *A. glarisianum* has between 20 and 25 anal fin elements, while in reality there are many more. It is clear, for example from specimen BMNH P3994 (Fig. 7.4c), that the first anal pterygiophore articulates

with the first haemal spine. This particular specimen has 67 caudal vertebrae and the anal fin stops only just anterior to the tail. In trichiurins the anterior part of the anal fin bears only very short rudimentary soft rays, which are, for most of their length, embedded in muscle and skin. Only close to the tail do the rays become longer and clearly visible. I think that Danil'chenko has overlooked this and only counted the long posterior anal fin elements. No scale covering.

Remarks. Agassiz (1833-44) identifies a few specimens as *Anenchelum longipenne* Agassiz, 1844, but does not describe them. Woodward (1901) includes *A. longipenne* in his synonymy of *Lepidopus glarisianum* with hesitation. I cannot state anything on the identity of these specimens in relation to either known Swiss *Anenchelum* (*A. glarisianum* and *A. brevicauda*), not having seen the specimens. Similarly, Woodward (1901) includes *Anenchelum breviceps* in his synonymy of *A. glarisianum* with hesitation, Danil'chenko includes *A. breviceps* without hesitation in his synonymy.

Here I synonymyse *Anenchelum angustum* with *A. glarisianum*. Danil'chenko (1980) described *A. angustum* as a separate species, stating it has 117-118 vertebrae. However, I counted in the holotype only 110 vertebrae. In PIN 3363-144, also labelled *A. angustum*, one can count 110 vertebrae. The caudal skeleton of that specimen is missing, so one cannot exactly know how many vertebrae the specimen had *in vivo*. PIN 3363-143 has 12 or 13 teeth in its dentary, which is perfectly in accordance with Danil'chenko's (1960) diagnosis of *A. glarisianus*. The specimens of "*A. angstum*" fit perfectly in the diagnosis of *A. glarisianum* and there do not seem to be any differences between them and *A. glarisianum*. Hence, *A. angustum* is considered a junior synonym of *A. glarisianum*.

Anenchelum paucivertebrale Bannikov & Parin, 1995 (Fig. 7.5)

Lepidopus sp. Bannikov (1993d): 245, fig. 3B. Type loc. river Pshekha, Russia, Eocene.

Anenchelum paucivertebrale Bannikov & Parin, 1995: 187, figs. 1-3. Type loc. *ibid.*

Diagnosis. Vertebrae 76-77 in number. The other *Anenchelum* species described here, *A. glarisianum*, has 106-116 vertebrae.

Referred specimens. PIN 4425-23 (**holotype,** Fig. 7.5), 4425-24 (**paratype**), 4425-25 (**paratype**) and 4425-28; river Pshekha, near Gornyy Luch village (Krasnodar territory), Cuacasus, Russia, Middle Eocene (Bartonian, Kuma Horizon).

Description. A detailed description is given in Bannikov & Parin (1995). Differences between their description and my observations are mentioned here. Fangs with clear barbs Pectoral fin rays 12 in number, 15 *sensu* Bannikov & Parin; spinous dorsal with XXX-XXXI spines, XXVII *sensu* Bannikov & Parin; soft

dorsal with 42 rays, 43 according to Bannikov & Parin; anal fin has certainly only I spine, not II.

cf. Anenchelum sp.

Lepidopus glarisianus Woodward, 1901: 479 (*pro parte*, no. 41811).

Diagnosis. Elongated fish with continuous dorsal fin, long pectoral fin (4 centra), large serial teeth and fangs.
Referred specimen. BMNH 41811, Engi, Canton Glarus, Switzerland, Early Oligocene: Rupelian (Glarnerschiefers).
Remarks. Together with a few other specimens, Woodward catalogued this specimen as *Lepidopus glarisianus*. However, an identification as *A. glarisianus* cannot be stated with certainty. On the specimen in question, it is not clear where the border is between the soft and hard part of the caudal fin (if preserved at all). Because of the distortion of the specimen, one cannot say with certainty if the poor association between dorsal pterygiophores and neural spines is natural or caused by distortion. It is likely, though that the specimen is indeed an *Anenchelum* and then probably an *A. glarisianum*, because every trichiurin from these Swiss Oligocene layers which have been named are *A. glarisianus*. I would like to be cautious about any identification, if I cannot be sure of the key apomorphies in the specimen, hence my assignment of this specimen to *cf. Anenchelum* sp.

GEMPYLINAE/TRICHIURINAE

Gen. et sp. ***incertae sedis*** (Fig. 7.6)
Diagnosis. Premaxilla and maxilla tightly bound, Straight, subconical teeth, fangs present, lower jaw protruding upper jaw.
Referred specimen. BMNH P10687, Delatyn, Galicia, Spain, Oligocene (Fig. 7.6).
Description. A slab of sediment with the remanants of a shattered skull. Left and right lower jaws well preserved, as are left upper jaw and anterior portion of right upper jaw. Teeth are well preserved: small, conical, with an unserrated cutting edge and without barbs. Left quadrate damaged but well preserved, associated to left lower jaw. Hyoid complexes preserved, although not well visible.
Remarks. Although catalogued as *Lepidopus*, this identification cannot be certified. The premaxilla and maxilla of the left upper jaw are tightly bound, which is a scombroid apomorphy. The lower jaw protrudes the upper jaw. The fangs are not well preserved, but in the anterior part of the left dentary and the premaxillae one can discern them none the less. Scombroids with conical teeth, fangs, and

protruding lower jaws are either gempylins or trichiurins. Gempylins have slightly caudad-curved teeth, whereas those in this specimen are straight. In scombroids, straight teeth seem to be the norm and only gempylins seem to have caudad-curved teeth. That condition is therefore interpreted as an apomorphy. It seems thus, that even though the dentition of this specimen resembles that of a trichiuriv in its straight teeth, it is a plesiomorpous dentition and cannot with certainty be assigned to a trichiurin. The specimen indeed possesses synapomorphies of the Gempylinae+Trichiurinae clade, but no specific trichiurin apomorphies.

Genus ***Eutrichiurides*** Casier, 1944

Trichiurides Winkler, 1876: 31 pl. II fig. 23 (*pro parte, non* fig. 22).

Lepidosteus Woodward, 1891b: 107 (*non Lepisosteus* Lacépède 1803).

Lophius Leriche, 1905: 172 (*non* Linnaeus, 1758).

Eutrichiurides Casier, 1944: 8, pl. figs. 8-12.

Diagnosis. Can readily be identified as a member of a Trichiurinae+Gempylinae clade by the following combination of characters: elongate skull, premaxilla-maxilla complex tightly bound, one or two large, curved premaxilla fang(s) (Fig. 7.6c), possessing small barbs, serial teeth straight (Fig. 7.6d). Genus *Eutrichiurides* identifiable by their comparatively large semiconical, elongate, stout erect teeth, slightly barbed at their apices. Fossil trichiurin *Casierichthys* with relatively small teeth. Other trichiurins with less differentiation between fangs and serial teeth, less fangs and/or fangs closer together. In *Eutrichiurides*, the serial teeth seem to be less compressed than in other trichiurins.

Type species. *Eutrichiurides delheidi* Leriche (1908).

Species composition. Seven species are known, from the Palaeocene to the Ypresian from Belgium, Morocco, Congo-Kinshasa and England. *Eutrichiurides winkleri* Casier, 1946 has been studied and is described below.

Remarks. *Eutrichiurides* has long been known as *Trichiurides* Winkler (1876). Casier (1944) noted that what was known as *Trichiurides* consists of two different genera, of which *Trichiurides* seems to be a merluciid and *Eutrichiurides* a trichiurin. Indeed, the large barbed fangs of *Eutrichiurides* are predominantly found in trichiurids, but some large specimens of gempylins also possess barbed fangs. All that can be said is that *Eutrichiurides* is not a gempylin, for it does not possess the apomorphous retrorse teeth: *Eutrichiurides* serial teeth are straight.

Eutrichiurides winkleri Casier, 1946 (Fig. 7.7).

Trichiurides sagittidens Winkler, 1876: 31 pl. II fig. 23 (*pro parte, non* fig. 22). Type loc. Schaerbeek, Belgium, Eocene.

Lepidosteus sp. Woodward, 1891b, 8: 107. Belgium, Lower Eocene

Lophius sagittidens , Leriche, 1905: 172. Type loc. Schaerbeek, Belgium, Eocene.

Trichiurides cf. *sagittidens* White, 1931: 87, pl. fig. 3 a-b . S-E England, Eocene.

Eutrichiurides cf. *delheidi*, Casier, 1944: 8, pl. figs. 8-12 (*non* Leriche, 1910). Type loc. Schaerbeek, Belgium, Eocene.

Eutrichiurides winkleri, Casier 1946: 144, pl. 6 fig. 19 a-b. Type loc. Schaerbeek, Belgium, Eocene.

Diagnosis. Seemingly one large premaxillary fang (possibly two) surrounded laterally, and followed, by smaller serial teeth with ovoid (semicircular) base. Other *Eutrichiurides* with more circular base. Dentary of *E. winkleri* seems straight, while dentary of *E. delheidi* seemingly curves ventrad at symphysis.

Referred material. The holotype, BMNH P26904 (**holotype**, skull, Fig. 7.6a, b, d), P21321-9 (47 teeth, Warden Point) and P26097-107 (14 teeth), Sheppey, England, Ypresian, London Clay; P49757 (Jaw fragment, *E.* cf. *winkleri*), Abbey Wood, England, Thanetian (Blackheath Beds, Oldhaven Formation), P65194 South England Middle Eocene: (Upper Barton Beds, Bartonian)

Description. Casier (1966) described the species in detail, based on BMNH P26904 and 217 loose teeth. Some inaccuracies were found in his description. See Remarks below.

Remarks. Based on the ovoid bases of the teeth of BMNH P26904's, compared to the perfectly circular base of *E. delheidi*'s teeth (Leriche, 1908), P26904 is a separate species *E. winkleri*. However, some remarks are to be made concerning Casier's (1966) description. He states that *E. winkleri* has a solitary, isolated fang in the premaxilla. However, this large fang seems to have been followed immediately by one of the numerous small premaxilla teeth and the fossil even suggests that the first fang preceded one other, most likely somewhat smaller (Fig. 7.6b). Furthermore, Casier (1966) stated that the dentary has a very blunt ending. The anterior tips of both dentaries are heavily damaged, so Casier's description is unfounded. Casier describes differences between the dentaries of *E. winkleri* and *E. delheidi* in a confusing manner. He writes that in the Eocene species, the dentaries do not have to be as high as in the other one (Casier, 1966, p. 245). I believe this puzzling description to mean that the dentary of *E. delheidi* is deeper than that of *E. winkleri*. (see Leriche, 1910, pl. XXV, fig. 1). Casier (1966) also fails to mention that the dentary of *E. delheidi* seemingly curves ventrad at symphysis (Leriche, 1910), whereas the dentary of *E. winkleri* seems straight (despite damage at symphysis). The most remarkable difference between the two

species however remains: the circular bases of *E. delheidi* teeth versus subconical bases of *E. winkleri* teeth.

Subfamily GEMPYLINAE Gill, 1862

Genus *Dicrotus* Günther, 1860

Gempylus Cuvier in Cuvier & Valenciennes 1832: 213, pl. 222 (*non* Cuvier, 1829).

Prometheus Lowe, 1838: 181 (*non* H¨übner, 1824).

Dicrotus Günther, 1860:349.

Acanthonothos Sauvage, 1870: 8 (*non* Gray, 1831).

Hemithyrsites Sauvage, 1873: 133, fig. 36 a-c.

Thyrsites Günther, 1873: 107, pl. 58, fig. 4 (*non* Lesson, 1830-1).

Promethichthys Gill, 1893: 115.

Diagnosis. Vertebral count of 33-35, a pectoral fin ray count of about 13, pelvic fin a single spine in adults, XVIII spines in the first dorsal fin, 13-19 rays in the second dorsal, II anal fin spines followed by 13-17 anal fin rays, 2 pairs of finlets, lateral line starting just ventral to first dorsal, behind pelvic fin curving ventrad steeply, then turning straight, perpendicular to axis of fish, until tail region. Differs from *Nealotus* (and most other gempylins) by a wavy, instead of a straight, lateral line. Differs from *Rexea* by a single instead of a double lateral line and a hypural complex with hypurals 1 and 2 autogenous as opposed to fused. Also differs from *Rexichthys* by lacking an anteroventral ramus of the ventral branch of the lateral line and possessing no more than two pairs of finlets (see Chapter 1).

Type species. *Dicrotus prometheus* (Cuvier, 1832).

Species composition. One Recent species, *Dicrotus prometheus*. Fossil species: *Dicrotus ?armatus* (Arambourg, 1925) (Sahelian, Late Miocene, Sicily) and *Dicrotus maicopicus* (Russia and Azerbaijan, Late Oligocene: Zuramakent and Abadzekh Horizons). Arambourg (1925) apparently did not consider his fossil species *Dicrotus armatus*, which he described as *Hemithyrsites armatus*, conspecific with *Dicrotus prometheus*, for which *Dicrotus armatus* is a junior synonym. It seems mere coincidence that Arambourg also assigned the epithet *armatus* to this species. I have not seen any specimens of Arambourg's *Dicrotus*. A description of *Dicrotus maicopicus* follows below.

Remarks. The nomenclatural history of this genus is long and complex. It is generally known as *Promethichthys* and fossil specimens have been referred to as *Hemithyrsites* Sauvage, 1873. The name *Dicrotus*, has appeared as a tentative synonym of *Promethicthys* (see Nakamura & Parin, 1993). I hereby propose to employ *Dicrotus* as the valid name for this genus, for reasons outlined below.

Palaeontologists have noted that what is known as *Promethichthys*, is the same as the fossil genus *Hemithyrsites* (Arambourg, 1925; Danil'chenko, 1960). Clearly, *Hemithyrsites*, published first by Sauvage (1873), has age preference over *Promtehichthys*, published by Gill (1893). Neontologists have seemingly failed to notice this and the name *Promethichthys* has remained in use for the only living species, *P. prometheus* (Cuvier, 1893) (Matsubara & Iwai, 1958; Parin & Bekker, 1972; Russo, 1983 and Nakamura & Parin, 1993). My comparison between a fossil "*Hemithyrsites*" (*Dicrotus maicopicus* (Danil'chenko, 1960)) and Recent "*Promethichthys*" (BMNH uncat., 1859.5.28.51, 1989.9.25.38; USNM 174934, 174935) have convinced me that these are indeed the same genera (see below). There is, however, an older valid name for this genus than *Hemithyrsites*. *Dicrotus armatus* Günther, 1860 is based on a young specimen, BMNH 1953.12.31.5 (Fig. 7.8). This young specimen is 58 mm long, devoid of scales, possesses a lateral line similar to those of adult "*Promethichthys*" (a single lateral line which is suddenly upturned anteriorly), it has XVIII first dorsal spines, which are long and serrated, a second dorsal formula of I or II+16 or 17, an anal fin with a formula II+16. Finlets are absent. Pelvic fin one single serrated spine, which is as long as maximum depth of body. The preoperculum possesses several spines at its posterior angle. This specimen is clearly a juvenile gempylin (deep, serrated dorsal fin, large serrated pelvics, spines on preoperculum, finlets not yet developed). The fin ray counts correspond perfectly with those of adult "*Promethicthys*" and so does the shape of the lateral line. In gempylins, this kind of lateral line is known only in "*Promethichthys*". Clearly, *Dicrotus* must be considered a name for a juvenile of *Promethichthys*, but since *Dicrotus* is the oldest valid name for the genus Günther (1860), I propose to employ this name instead of *Promethicthys* The latest International Code for Zoological Nomenclature (International Commission, 1999) does not mention that names given to adult specimens have preference over those allocated to juveniles. Because of the rule of age preference, thus, *Dicrotus* has to be adopted. Since *Dicrotus* has no major importance in the fishery industry (Nakamura & Parin, 1993) I suppose that there are no reasons to maintain the name *Promethichthys* because of it being an important widespread name in commercial circles.

Dicrotus maicopicus (Danil'chenko, 1960) (Fig. 7.9)

Hemithyrsites maicopicus Danil'chenko, 1960: 140, fig. 28, Plate XIII, figs. 1-2. Type loc. Kurdzhips River, Russia, Oligocene.

Hemithyrsites maicotext-figus Bannikov, 1997: 140 (*typ. err.*).

Diagnosis. Thirty-five vertebrae, Reduced pelvic fin: one well developed spine (found in *H. armatus*: Arambourg, 1925). Differs from *Nealotus* by having less (35 as opposed to 36-37) vertebrae. Some *Rexea* species also have a pelvic fin reduced to one spine; these species have only 34 vertebrae. *Dicrotus prometheus* has a poorly developed pelvic spine. In larger *D. prometheus* specimen the pelvic spine is missing altogether (Nakamura & Parin, 1993).
Referred specimen. PIN 848-131, **Holotype**, Kurdzhips River, Russia, Late Oligocene: Chattian (Zuramakent Horizon) (Fig. 7.9).
Description. *D. maicopicus* is described in detail by Danil'chenko (1960). Meristic counts of the studied specimens and differences from Danil'chenko's ovbservations are given here. Two counterparts of a small specimen, fork length 53 mm, total length 59 mm. Orbit large, diameter slightly shorter than preorbital region and slightly longer than postorbital region. Pterotic a short wing. Total number of vertebrae observed 35 (32-33 according to Danil'chenko, 1960, but his 15-16+16-17 vertebrae should have been a total of 31-33; 33-34 according to Danil'chenko, 1980). Caudal fin with 25 lepidotrichia. Number of pectoral fin rays not known from specimen, reported as 13-15 in Danil'chenko (1960). Pelvic fin reduced: one well developed fin spine, longer than pelvic projection. First dorsal fin consisting of XVII rigid spines. Second dorsal fin with 13 soft rays, preceded by one spinous ray. Proximal-middle and distal radial of soft dorsal fin pterygiophore overlap extensively, distal radial locks snugly on process of proximal-middle radial. Number of soft anal fin rays not known, but preceded by two thick spines. Two pairs of finlets (dorsal and anal).

Genus *Rexea*

Gempylus Cuvier in Cuvier & Valenciennes 1832: 215 (*non* Cuvier, 1829).

Thyrsites Bleeker, 1856: 42 (*non* Lesson, 1831).

Prometheus Gill, 1863: 329 (*non* Lowe, 1838).

Rexea Waite (1911): 49.

Jordanidia Snyder, 1911: 527.

Diagnosis. Vertebral count of 33-35, pelvic fin a single spine in adults, two pairs of finlets, lateral line double. Differs from *Nealotus* and *Dicrotus* by a double instead of a single lateral line. Differs from *Dicrotus* by and a hypural complex with hypurals 1 and 2 fused as opposed to autogenous. Also differs from *Rexichthys* by lacking an anteroventral ramus of the ventral branch of the lateral line and possessing no more than two pairs of finlets (see Chapter 6).

Type species. *Rexea antefurcata* Waite, 1911 (Recent).
Species composition. One fossil has been found, which cannot be specifically identified (see below). Six Recent species are known (see Parin, 1989; Nakamura & Parin, 1993).

***Rexea* sp.** (Fig. 7.10)

Referred specimen. BMNH P37337, Asmari Mountain, Masjid-i-Sulaiman, Iran, Eocene? (Fig. 7.10).
Diagnosis. Dentary and premaxillary teeth retrorse, Large orbit, slightly shorter than preorbital region. Pelvic fin spine accompanied by three soft rays. Differs from *Gempylus* by having a less rounded orbit and more robust jaws. Differs from *Dicrotus* and many *Rexea* species by having soft rays besides pelvic spine.
Description. Skull long. Neurocranium shallow, with skull roof making small angle with horizontal axis of fish. No cranial crest. Eye socket large, diameter slightly less long than preorbital region and slightly longer than postorbital region. Dentary gradually tapering rostrad, up to strongly narrowed anterior symphysis. Relatively large triangular teeth, slightly retrorse. Angular/articular abruptly narrowed caudally. Pectoral fin with 13 rays. Pelvic fin inserted on long slender pelvic plate (Fig. 7.10). Although badly preserved, seemingly two pelvic fins, each consisting of I spine and three soft rays, present. Pelvic spine longer than pelvic projection. First pterygiophore of dorsal fin seemingly inserted in second interhaemal space.
Remarks. Recent gempylins with reduced pelvics (I spine and < 5 soft rays) are found in *Gempylus* and *Rexea*. The morphology of this skull comes closer to *Rexea* than it does to *Gempylus* (see diagnosis). Of all *Rexea*, only *Rexea brevilineata* Parin, 1989 and *Rexea solandri* (Cuvier, 1832) possess 2-3 soft pelvic fin rays. In other *Rerxea* species the pelvic consists only of one spine. The only relevant specific character this specimen seems to be the number of pectoral fin rays (13). *R. brevilineata* has (13-) 14 rays and *R. solandri* has (13-) 14 (-15) rays (Nakamura & Parin, 1993). Hence, this character is inconclusive. BMNH P37337 could be either of these species or an as yet undescribed one. This is the first ever fossil assigned to *Rexea*.

Subfamily *cf.* GEMPYLINAE

Genus *Abadzekhia* Bannikov, 1985

Scombrosarda Bannikov, 1980: 45 (*nomen nudum*).

Abadzekhia Bannikov, 1985: 44, text-figs. 17v, 21, 22, plate V, figs. 2, 3.

Diagnosis. Possesses large scales and one pair of premaxillary fangs.
Type species. Only one species known, described below.
Species composition. The type species only.
Remarks. When first described, Bannikov (1985) included *Abadzekhia* (Fig. 7.11) within subfamily Scomberomorinae, family Scombridae. Reasons for that placement were the presence of finlets, a deep body, and relatively few vertebrae. However, it was suspected as well (Bannikov, 1985) that *Abadzekhia* is related to gempylins or euzaphlegids. Characters that fuelled that suspicion were the non-hypurostegic tail (which is in fact a symplesiomorphy) and the presence of a premaxillary fang (Fig. 7.11c). Bannikov & Fedotov (1989) evaluated "..the taxonomic value of the characters in *Abadzekhia*..." (translation by N. Bakhurina), as a consequence of which they ascribe this genus to the gempylins. I agree with Bannikov & Fedotov (1989) that *Abadzekhia* resembles gempylins such as *Ruvettus* and *Lepidocybium* in a deep body, the presence of finlets and a reduced battery of fangs (only one in each premaxilla in *Abadzekhia*). The affinity of *Abadzekhia* with gempylins seems to be confirmed by a strong synapomorphies: the modified dorsal pterygiophores (see below) and slightly retrorse serial teeth. This was not remarked by Bannikov (1985) and Bannikov & Fedotov (1989), but to me these are the strongest signals that *Abadzekhia* could be a gempylin. *Abadzekhia*'s large scales are not seen in any Recent gempylin. *Abadzekhia* seems to be closely related to *Palimphyes*, another gempylin-like fish (see also description of *Palimphyes*, below), based on similarities in the caudal skeleton: both have two small hypural plates (fusion of hypurals 1-2 and 3-4 respectively). The affinities of *Palimphyes* are not clear, in that it lacks fangs. The presence of fangs is a gempylin apomorphy.

Abadzekhia marinae Bannikov, 1985

Scombrosarda miatlica Bannikov, 1980: 45 (*nomem nudum*).

Abadzekhia marinae Bannikov, 1985: 44, text-figs. 17v, 21, 22, plate V, figs. 2, 3. Type loc. river Belaya, Russia, Oligocene.

Diagnosis. As for genus.
Referred material. PIN 1413-81 (**holotype**, Fig. 7.11a), 1413-82 (two counterparts, Fig. 7.11b, c) and 1413-83 (**paratype**); river Belaya, near Abadzekhskaya village, Caucasus, Russia, Late Oligocene: Chattian (Morozkina Ravine Horizon).

Description. A detailed description is given in Bannikov (1985). Comparisons between my observations and Bannikov's description are given below. Serial teeth slightly retrorse. Procurrent spur absent. First dorsal pterygiophore inserted in second interneural space. Elements that make up pterygiophores cannot be identified. However, it is clear that pterygiophores are enlarged and overlapping. I interpret this as the modified configuration of dorsal pterygiophores, as seen in gempylins and trichiurins (see Chapter 5). Meristic count of XV first dorsal spines (Bannikov, 1985) difficult to verify. In damaged first dorsal of the holotype I could recognise XI spines. Bannikov recognised 11 soft rays in the second dorsal fin. I counted 10 in the holotype. Anal fin I spine, 9-10 rays. Finlets five in number (4-6 according to Bannikov, 1985).

Genus ***Palimphyes*** Agassiz, 1844.

Clupea De Blainville, 1818: 315 (*non* Linnaeus, 1758).

Palimphyes Agassiz, 1833-44: 46.

Krambergia Simionescu, 1905: 114.

Dipterichthys, Arambourg, 1967: 123.

Diagnosis. Pectoral fins long, often reaching up to second dorsal fin. Dorsal fins separated, not closely adjoined.

Type species. *Palimphyes elongatus* (De Blainville, 1818)

Species composition. Only fossil species are known, found in the former USSR, around the Caucasus region, from the early Tertiary to the Rupelian (Early Eocene), and the Rupelian of Switzerland, Romania and Iran. I have studied good specimens of *Palimphyes chadumicus* Danil'chenko, 1960; *P. elongatus*, *Palimphyes palaeocaenicus* Danil'chenko, 1968 and *Palimphyes psehkhaensis* Bannikov, 1993c. Of *Palimphyes pinnatus* Danil'chenko, 1962 I have seen only the holotype (PIN 1413-77), which is a badly preserved specimen. I did not feel confident I could rely on that specimen to describe this species. Two figures of the holotype exist (Bannikov, 1993c; Danil'chenko, 1962). P.G. Danil'chenko, or his illustrator who made the figures, managed to extract much detail from a badly preserved specimen, which on the figures resembles indeed a *Palimphyes*. According to Bannikov (pers. comm., 1997) much better preserved specimens of this species exist, which I, unfortunately, have not seen.

Remarks. *Palimphyes* is normally understood to be part of the Euzaphlegidae (see David, 1943; Danil'cheko, 1960). I believer, however, that the euzaphlegids are polyphyletic and therefore invalid as a taxonomic entity. *Palimphyes* possesses pterygiophores that overlap strongly to form a chain-like structure. However, it lacks premaxillary and dentary fangs, which are gempylin synapomorphies.

Palimphyes chadumicus Danil'chenko, 1960 (Fig. 7.12).

Palimphyes chadumicus Danil'chenko, 1960: 137, text-fig. 27, pl. XIII, figs. 3, 4. Type loc. North Osetiya, Russia, Oligocene.

Referred material. PIN 290-3 (**Holotype**), 290-8, (**Paratype**), North Osetiya, 3363-136 and 3363-137, river Belaya, North Caucasus, Russia, Early Oligocene: Rupelian (Khadum deposits).

Diagnosis. First dorsal pterygiophore is inserted in fifth interneural space. Inserted in third interneural space in other *Palimphyes*. Although Danil'chenko (1960) describes it as a new species, a diagnosis for *P. chadumicus* or comparisons with other *Palimphyes* are not mentioned.

Description. Species described in detail in Danil'chenko (1960). Observations of mine that differ with Danil'chenko's are noted below. Ceratohyal ventrally smooth and straight. Vertebrae 36-39 (38-39 in Danil'chenko, 1960) in number. Caudal fin with 30-34 lepidotrichia. Procurrent spur absent. Pelvic fin longer than pelvic projection. First dorsal with VIII-X spines (VIII in Danli'chenko, 1960), second dorsal I+17 (I+18-29 in Danil'chenko, 1960; corrected to 18-20 in Danil'chenko, 1980). Pelvic plate simple, not differentiated into different wings.

Palimmphyes elongatus (De Blainville, 1818) (Fig. 7.13)

Clupea elongata De Blainville, 1811: 315. Type loc. Canton Glarus, Switzerland, Oligocene.

Palimphyes longus Agassiz, 1833-44: 46, pl. 19. Type loc. *ibid.*

Palimphyes brevis Agassiz, *l.c.*: 47, pl. 20; 21, figs. 1, 2. Type loc. *ibid.*

Palimphyes latus Agassiz, *l.c.*: 48, pl. 28, fig. 1. Type loc. *ibid.*

Palimphyes crassus Giebel, 1847: 666. Type loc. *ibid.*

Palimphyes gracilis Giebel, 1847: 667. Type loc. *ibid.*

Palimphyes glaronensis Wettstein, 1886: 88, pl. II, figs. 1-6. Type loc. *ibid.*

Referred material. BMNH uncat. and 41821, Engi, Canton Glarus, Switzerland, Early Oligocene: Rupelian (Glarnerschiefers).

Diagnosis. Pectoral fins with 11 rays (13-20 in other species).

Description. This species is described in detail by Agassiz (1833-44, as *P. longus*, *P. brevis* and *P. latus*) and Wettstein (1886) as *Palimphyes glaronensis*.

Remarks. Wettstein (1886) took the taphonomic distortion of the various Swiss *Palimphyes* fossils into account and realised that the different eptihets employed by Agassiz (1833-44) belong to the same species, which he named *Palimphyes glaronensis*. Woodward (1901) realised that the species was originally described as *Clupea elongata* De Blainville 1818, and thus correctly described the species as *Palimphyes elongatus*.

Palimphyes cf. elongatus

Palimphyes elongatus Woodward, 1901: 461 (*pro parte*, BMNH P4952).

Referred material. BMNH P4952, Plattenberg, Canton Glarus, Switzerland, Early Oligocene: Rupelian (Glarnerschiefers).

Diagnosis. Body covered by large cycloid scales, dorsal fins well separated by spineless/rayless pterygiophores, 35 or more vertebrae.

Description. A nearly complete impression of a single fish in a thin plate of slate. The anteriormost part of the individual is missing. Unidetifiable skull bones are scattered on the piece of slate, but they can only be identified as being skull bones. 35 Vertebrae are preserved, but the vertebral count could well have been higher. Vertebrae not well constricted medially. Neural and haemal spines stout. Hypural formula not exactly clear, but a ventral and dorsal hypural plate present. Parhypural autogenous. No hypurostegy. Caudal fin with 29 lepidotrichia. First dorsal with at least nine spines, followed by four "empty" pterygiophores. These empty pterygiophores are followed by a second dorsal fin consisting of 18 or 19 elements, the first of which is probably a spine, followed by soft fin rays. Pelvic fin with one spine and five soft rays. Anal fin with II spines and 16 soft rays. Body completely covered by large cycloid scales.

Remarks. The specimen contains the diagnostic features of a *Palimphyes*, but its specific identity cannot be detrmined. The meristic counts of the possibly incomplete vertebral column and first dorsal fin do not contradict an assignment to *P. elongatus*, but do not confirm it either. The only *Palimphyes*-species known from the Rupelian of Switzerland so far is *P. elongatus* (Wettstein, 886); Woodward, 1901; Bannikov, 1993).

Palimphyes palaeocaenicus Danil'chenko, 1968 (fig. 7.14)

Palimphyes palaeocaenicus Danil'chenko, 1968: 143, text fig. 2, pl. XXXIV, figs. 1, 2. Type loc. Uilya-Kushlyuk, Turkmenistan, Eocene

Referred material. PIN 2179-83 (**holotype**) Uilya-Kushlyuk village, Turkmenistan, Ypresian, (Middle Danatinsk Svita).

Diagnosis. Vertebrae 32 in number (≥ 35 in other species), pectoral fins with 13 rays (11 in *P. elongatus*, ≥16 in other species), 16 anal fin rays (more in other species).

Description. Species described in detail by Danil'chenko (1980). Different observations indicated here. Danil'chenko noted 32 vertebrae in total. In the holotype, the anteriormost section of the vertebral column and the head are missing. Only 28 or 29 vertebrae are preserved. Anal fin with 14-15 rays in Danil'cheko

(1980), 16 according to my observations. Pectoral fin with 14-16 rays according to Danil'chenko, but I counted 13 in holotype.

Remark. In Bannikov (1985), the Danatisk Svita was regarded to be Late Palaeocene, but later it was shown that the fish beds from which these fossils originate are of the Middle Danatinsk, which is Ypresian (Harland *et al.*, 1990; Tyler & Bannikov, 1992). The Ypresian is of Early Eocene age.

Palimphyes pshekhaensis Bannikov, 1993 (fig. 7.15)

Palimphyes pshekhaensis Bannikov, 1993c: 98, figs. 1, 2.

Referred material. PIN 4425-7 (**paratype**, fig. 7.15b) and PIN 4425-12 (**holotype**, Fig. 7.15a), Krasnodar territory, river Pshekha, 1 km upstream from Gornyy Luch Farm, Caucasus, Russia, Bartonian (Kuma horizon).

Diagnosis. Vertebrae 37 in number (32 in *P. palaeocaenicus*, 38-39 in *P. elongatus*)

Description. Bannikov (1993c) gives a detailed description of this species, in which he states that the pectoral fin of this species points ventrad. I found that the so-called ventrad-pointed pectoral fins are dislocated, and I suspect that *in vivo* these fins would have pointed posteriorly, as in other scombroids (except *Xiphias*, in which pectoral does point ventrad). Bannikov (1993c) mentioned the caudal fin has 17 principal rays. According to my observations there are in total 29 (holotype) or 31 (paratype) rays, including procurrent ones. Bannikov (1993c) mentions pectoral fin has ≥ 12 rays, according to my observations there are ~17 (holotype) and 20 (paratype). I counted 19 second dorsal rays, according to Bannikov (1993c) there are 20.

Genus ***Progempylus*** Casier, 1966

Percidae? cf *Planesox*, Woodward, 1901: 519.

Progempylus, Casier, 1966: 250.

Diagnosis. Dentary teeth, curved strongly posteriorly, elongated slender skull, orbit almost circular, region of skull containing supraoccipital, parietals and epiotics considerably elevated (Fig. 7.16). In *Gempylus*, this region is rather flat.

Type species. Only one species, described below.

Species composition. Only the type species.

Remarks. Mainly due to the retrorse conical teeth, the affinities of *Progempylus* seem to lie within the gempylins. In the cladogram of scombroids presented in Chapter 8 however, its phylogenetic position remains uncertain.

Progempyus edwardsii Casier, 1966 (Fig. 7.16)

Percidae? cf *Planesox vorax*, Woodward, 1901: 519

Progempylus edwardsii, Casier, 1966: 250. Type loc. Sheppey, England, Eocene.

Diagnosis. As for genus.

Referred material. BMNH 3288, **Holotype**, Sheppey, England, Early Eocene: Ypresian (London Clay).

*Description.*Casier (1966) described *P. edwardsii* in great detail.

Remarks. Casier (1966) was the first to assign the name *P. edwardsii* to this species. Woodward (1901) described the holotype of this species as "probably belonging to the Percidae", but being very close to *Planesox vorax* Owen, 1854. The discussed specimen cannot possibly be assigned to *Planesox*. Although seemigly matching Owen's (1854) description up to a certain point, the skull of *Progempylus* is less complete than Owen's original material, so some of *Planesox*' characters cannot be found in this *Progempylus*, The "type" of Owen's description is missing. Thus, it ican never be verified if the fossils in question are *Planesox vorax*. I follow here Casier's suggestion of adopting the generic name *Progempylus* for this specimen.

?Gempylinae indet. (Fig. 7.17)

cf. *Eutrichiurides* Casier, 1966: 249, fig. 56.

Referred material. BMNH 41318 (skull), Sheppey, England, Early Eocene: Ypresian (London Clay), labelled as "?*Eutrichiurides*" (Fig. 7.17).

Diagnosis. Cranium similar to that of a Scombrinae (*Scomber*, *Rastrelliger* and probably †*Scombrinus*), but more elongated, pattern of cranial ridges similar to those in gempylins.

Description. Only briefly described in Casier (1966) More detailed description follows here. Damaged cranium. Elongated skull, about 133 mm long. The most rostral parts of ethmoidal complex and vomer missing. Orbit somewhat ovoid, longer than deep, its dorsal ridge somewhat flattened. Frontals strongly constricted above middle of orbit. Suture between frontals slightly undulating. Frontal slightly depressed directly adjacent to suture. This depression broadens and deepens gradually posteriorly. Supratemporal groove short, extending just into frontal and anteriorly bordered by ridge which slants posteriorly towards axis of cranium. Anterior borders of left and right suprqatemporal groove meet above axis of cranium. Epiotic ridges almost straight, extending anteriorly as lateral borders of supratemporal groove. Lateral groove of skull, laterally bordered by pterotic groove also short. Postero-superior fossa well posterior of middle of orbit. Posttemporal

region of skull relatively long: lenght of the part of supraoccipital crest distal to point where epiotics meet an estimated 22% of total skull length. Supraoccipital crest damaged. Parasphenoid almost straight, slightly slanted ventrad posteriorly.

Remarks. Casier (1966) was the first to describe this cranium and believed it could belong to the genus *Eutrichiurides*, based on that it shows a combination of characters of Scombrinae and Trichiurinae (mainly *Lepidopus*). Casier believed that *Eutrichiurides winkleri* (described above) shows a mixture of trichiurin and scombrin characters, but the scombrin characters are not based on any clear apomorphies, but on superficial resemblances such as the shape of the articular. In *Eutrichiurides winkleri*, the cranium is virtually unknown, whereas BMNH 41318 is a cranium, without branchiocranium. I am thus very suspicious of the description of this specimen under the heading "*Eutrichiurides*". Furthermore, Casier contradicts himself when he states that *Eutrichiurides* shows a combination of characters of both scombrins and tichiurids, because he places *Eutrichiurides* in the Trichiuridae. Cranium 41318 resembles a trichiurin canium, in that it resembles an elongated scombrid cranium with large orbits. However, most gempylin skulls can also be thus typified. Although this cranium superfically resembles that of a *Lepidopus* it is clearly not one. The fossil lacks a distinct cranial crest, present in *Lepidopus*. Recent trichiurins without cranial crest are *Aphanopus* and *Benthodesmus*. However, since the absence of a crest is a plesiomorphy, this cranium, cannot be readily assigned to either trichiurin and lacks any other clear synapomorphies with both *Aphanopus* and *Benthodesmus*. Judging by general shapes of skulls and patterns of dorsal cranial ridges, this "*Eutrichiurides*" resembes more a gempylin than it does a trichiurin (see Figs. 7.17a, d, e). However, I do not feel that there are apomorphies which are strong enough to assign this skull to either a gempylin or a trichiurin, also since the pattern of cranial ridges does not seem well quantifiable to express differences between trichiurins and gempylins. Cranium BMNH 41318 superfically resembles *Progempylus edwardsii*. However, *Progempylus* and this fossil do not share any unique character (combinations). The parietal, epiotics and supraoccipital are elevated much higher over the frontals in *Progempylus* than in this cranium (compare Figs. 7.16c, 7.17c). The only concrete thing that can be said about BMNH 41318 at the moment is that it resembles a gempylin, but might as well represent an (unknown) trichiurin.

Family **SCOMBRIDAE**, Rafinesque, 1815

Subfamily **Scombrinae**, Rafinesque, 1815

Genus ***Scomber*** Linnaeus, 1758

Scomber Linnaeus, 1758: 291.

Pneumatophorus Jordan & Gilbert, 1883: 593.

Irifera Jordan, 1927: 97.

Diagnosis. Generally 31 (sometimes 30) vertebrae, hypural plate element fusion pattern: 1-2, 3-4, 5; hypurostegy, vomer and palatines toothless, lachrymal larger than diameter of orbit. Differs from highly resembling *Rastrelliger* through being more slender, not having lost the anal fin spine, having 12-28 first dorsal interneural bones with a crown-like dorsal structure, contrary to 10-11 with a plate-like dorsal structure in *Rastrelliger*, first haemal spine not hooked as in *Rastreliger* and the last branchiostegial ray not broadened and flattened like in *Rastrelliger* and gill filaments never visible through open mouth, as in all *Rastrelliger* but *Rastrelliger faughni* Matsui, 1967.

Type species. *Scomber scombrus* Linnaeus, 1758 (Recent).

Species composition. Recent forms known are *Scomber australasicus* Cuvier, 1831; *Scomber japonicus* Houttuyn, 1782 and *S. scombrus*. Fossil forms are known from the Eocene to Pliocene of Europe and Africa, the Miocene of North America and the Tertiary of East Asia. A few species, based on otoliths only are mentioned by Landini & Bannikov (1983).

Remarks. Bannikov (1985) included *Auxides* (=*Scombrinus*); *Turio* Jordan & Gilbert, 1920 and *Thyrsion* Jordan & Gilbert, 1920 in his synonmy of *Scomber*. All three diagnoses are incorrect. *Scombrinus* is described in more detail above. The body of *Scombrinus* is completely covered by relatively large scales, without a corselet. The scales of *Scomber* are small. Also, the two dorsal fins of *Scombrinus* are close together. *Turio* is a primitive scombrid fish, but is not synonymous with *Scomber*. First, *Turio* has 28 vertebrae (Jordan & Gilbert, 1920; Jordan, 1921), as opposed to *Scomber*'s 30-31, its first dorsal fin contains 20 spines and is close to the second dorsal (Jordan & Gilbert, 1920; Jordan, 1921), whereas *Scomber* possesses 9-13 first dorsal rays and there is a large interspace between the first and second dorsal. *Thyrsion*, which is the valid genus epithet for what is otherwise known as *Thyrsocles*, possesses 46 or more vertebrae. *Thyrsion* does not possess a hypurostegic caudal fin.

Scomber and *Rastrelliger* are easily confused scombrid genera. The characters that Bannikov (1985) has used to identify the Caucasus specimens as *Scomber* are inadequate: the vomers and palatines of the specimens are not (well enough) preserved and neither are the gill filaments. However, an assessment of the body depth, as used by Bannikov (1985) is sometimes useful. Other characters, like the curvature of the first haemal spine (see § 5.2.2.4) and the number of first dorsal interneural bones are well preserved and are good diagnostic characters. All Caucasus specimens are, based on these characters, identified as *Scomber*.

Scomber cubanicus Danil'chenko, 1960 (Fig. 7.18)

Scomber cubanicus Danil'chenko, 1960: 154, fig. 31, pl. XVI, figs. 1-2. Type loc. Khadyzhenskaya Cossack village, Russia, Oligocene.

Diagnosis. Space between dorsal fins longer than length of first dorsal fin. 15 Interneural bones, 14 precaudal vertebrae.

Referred material. PIN 484-11, **holotype**, Khadyzhenskaya Cossack village, Krasnodar territory, Caucasus, Russia, Late Oligocene: Chattian (Riki Horizon), PIN 2180-11, Pirekishkyul' village, Azerbaijan, Late Oligocene: Chattian (Abadzekh Horizon).

Description. Detailed description given in Bannikov (1985). Different observations and additional information given here. Small fossils. PIN 2180-11 has forklength of 33 mm. Vertebrae 31, of which 14 precaudal. Hypural plate coverded by caudal fin (hypurostegy) with 33 soft rays, no procurrent spur. Pectoral fins slightly directed postero-dorsal, with 15-17 rays (16-17 according to Bannikov). Pelvic fin longer than pelvic projection. Dorsal fins not connected. Space between dorsal fins slightly longer than length of first dorsal. First dorsal with IX-XIII (IX-X according to Bannikov) spines, followed by five rayless pterygiophores. First dorsal less deep than head, depth declining rather abruptly caudad. Second dorsal fin with 14 soft rays (I+9-10, accrding to Bannikov). Anal fin with II hard spines and 11 (10-11 *sensu* Bannikov) soft rays. Six anal and dorsal finlets. Body covered with small scales, which are larger anteriorly, but do not form clear corselet.

Scomber gnarus Bannikov, 1979 (Fig. 7.19)

Scomber colias Smirnov, 1936: 64, pl. VII, fig. 34 (*non* Gmelin, 1789). Yp. loc. river Pshekha, Azerbaijan, Oligocene.

Scomber japonicus : Danil'chenko, 1960: 157, pl. XII, fig. 2 (*non* Houttuyn, 1782). Type loc. *ibid.*

Scomber gnarus Bannikov, 1979: 100, fig. 2. Type loc. *ibid.*

Diagnosis. Space between first dorsal; and second dorsal slightly less than length of first dorsal. Twenty first dorsal pterygiophores, of which VIII-XI bear spines, 14 precaudal vertebrae.

Referred material. PIN 1413-34, river Chyorna, Azerbaijan, Oligocene (Zuramakent Horizon); 3363-27, **holotype**, river Pshekha in Shirvanskaya village, North Azerbaijan, Late Oligocene: Chattian (Voskovorskiy Horizon); PIN 3363-36, 3363-38, 3363-40, 3363-41, 3363-43, 3363-44, 3363-45, 3363-46, 3363-47, 3363-48, river Pshekha, in Shirvanskaya village, Azerbaijan, Early Miocene

(Voskovogor Svita); PIN 2180-9, 2180-10, Pirekishkyul' village, Azerbaijan, Early Miocene (Sulak Svita); PIN uncatalogued (labelled as *Scomber japonicus*).

Description. Detailed description given by Bannikov (1985). Different observations and addtional data given here. Slender fish with pointed head. Most specimens between 100 and 200 mm fork lenght. The largest specimen known is an uncatalogued PIN specimen of 462 mm total length. Ventrally, ceratohyal smooth and straight. Hypural plate cosisting of two smaller "subplates" (hypurals 1-2 and 3-4), hypural 5 and parhypural autogenous. Hypural plate coverded by caudal fin (hypurostegy) with 26-35 soft rays, no procurrent spur. Pectoral fins slightly directed dorso-caudad, with 13-14 (18-20 according to Bannikov) rays. Pelvic fin with 1 hard spine and 5 soft rays. Pelvic fin longer than pelvic projection. First dorsal pterygiophores 20 in number, of which 8-11 (11-12 *sensu* Bannikov) bear spines. First dorsal less deep than head, depth declining rather abruptly caudad. Second dorsal fin with 11-16 (I+11 according to Bannikov) soft rays. Anal fin with I-II hard spines and 10-12 soft rays (I+10-11 according to Bannikov). Four to six anal and dorsal finlets (Five according to Bannikov). Body covered with small scales, which are larger anteriorly, but are not developed into corselet.

Scomber voitestii Paucă, 1929

Scomber oligocenicus Paucă, 1929a: 117.

Scomber voitestii Paucă, 192b: 212, fig. 1.

Diagnosis. Space between dorsals longer than first dorsal, 12 first interneural bones, 14 precaudal vertebrae.

Referred material. PIN 491-10 and 491-11, North Pasechnaya, Predcarpathians, Ukraine, Early Oligocene: Rupelian (Menilite Svita).

Description. Detailed description given in Bannikov (1985). Different observation and additional information given here. No procurrent spur. Pectoral fin with 15 rays. Pelvic fin longer than pelvic projection. Space between dorsal fins slightly longer than length of first dorsal. First dorsal with IX spines (VIII according to Bannikov), followed by four rayless pterygiophores First dorsal less deep than head, depth declining rather abruptly posteriorly. Second dorsal fin with 12 (I+10-11 *sensu* Bannikov) soft rays. Anal fin with II hard spines and 10 (11-13, according to Bannikov) soft rays. Five Anal and dorsal finlets. Body covered with small scales, which are larger anteriorly, but are not developed into corselet.

Remark. This species was first described as *Scomber oligocenicus* Paucă, 1929, and indicated to be found in the Early Oligocene of Romania, Hungary and Ukraine. It is acknowledged, in synonymy lists, that this is the same species as *S.*

voitestii (Danil'chenko, 1960; Bannikov, 1985) but a reason was not given why the earlier name was rejected. I have not found Paucă's original descriptions myself. I maintain here the name *S. voitestii* , assuming good reasons for authors for rejection of *S. oligocenus*, until I find a reference where acceptable reasons for the rejection are given. This species is called *S. voitestii* in amongst others Danil'chenko (1960, 1980), Jerzmańska (1968) and Bannikov (1985).

Genus **indet.**

Diagnosis. Forntals with crests that form triangle with apex just anterior of supraoccipital, and posteromedian depression.

Referred specimens. BMNH P23969 (originally labelled as Scombrid?), Skarrehage Pit, Island of Mors, Denmark, Early Eocene: Ypresian (Mo-Clay Formation) and PIN 3363-142 (stored as *Scombrosarda* cf. *cernegurae*).

Description. Arrowhead-shaped craniums with relatively long pterotic spine, frontals concave directly anterior of supraoccipital. The Russian specimen possesses lachrymal which is longer than orbit diameter, and crescent-shaped preoperculum.

Remarks. These specimens concern impressions of the dorsal side of the cranium and in the case of the Russian specimen, also appendages to the cranium. The impressions are very mackerel-like. It is not clear, however, if they belong to *Scomber*, *Rastrelliger*, or *Scombrinus*. The cranium itself does not supply any apomorphies that characterise any of these highly resembling genera. Also, characters such as the crescent-shaped preoperculum and the large lachrymal do not distinguish between *Scomber*, *Rastrelliger* and *Scombrinus*.

cf. Subfamily **SCOMBRINAE**

Genus *Scombrinus* strongly resembles the Recent mackerels *Scomber* and *Rastrelliger*. It differs from these by having larger scales and their dorsal fins closely adjoinned. It seems likely that *Scombrinus* is a primitive sister taxon of *Scomber* and *Rastrelliger*, but the cladistic analysis (Chapter 8) leaves its phylogenetic position unresolved.

Genus ***Scombrinus*** Woodward, 1901

Scomber Volta, 1796: 66, pl. xiv, fig. 2; Volta, 1796 :125, pl. 29, fig. 2 (*non* Linnaeus, 1758).

Ophicephalus Volta, 1796: 193, pl. xlviii (*non* Bloch, 1793).

Labrus Volta, 1796: 204, pl. l, fig. 1 (*non* Linnaeus, 1758).

Cybium Agassiz, 1835: 293 (*non* Cuvier, 1829).

Thynnus Agassiz, 1833-44: 55, pl. 27 (*non* Cuvier, 1817).

Scombrinus Agassiz, 1845: 308 (*nomen nudum*).

Scombrinus Woodward, 1901: 461.

Auxis? Woodward, 1901: 464 (*non* Cuvier, 1829).

Auxides Jordan & Gilbert, 1919: 10, pl. V, fig. 2.

Scombrosarda Danil'chenko, 1962: 122.

Grammatorcynus Arambourg, 1967: 14, fig. 52, pl. XIII, figs. 2, 3 (*non* Gill, 1862).

Pinulothunnus Ciobanu, 1970[5]: 83.

Diagnosis.Completely covered by relatively large scales, no corselet, two dorsal fins close together, hypural plate split in a dorsal and a ventral plate, 31 vertebrae, of which 17 caudal. Resembles *Scomber* and *Rastrelliger*. These, however, have widely separated dorsal fins.

Type species. *Scombrinus nuchalis* Woodward, 1901.

Species composition. Two species are known from the United States: *Scombrinus sanctae-monicae* (Jordan, 1919) and *Scombrinus bruntoni* (Jordan, 1921) (both known as *Auxides*, Early Miocene/Oligocene, Southern California, U.S.A.) and *Scombrinus scomberoides* (Arambourg, 1967) (known as *Grammatorcynus*, South Iran, Middle Oligocene). These species have not been studied. Numerous species are known from Italy, England, Iran and the former USSR which are described below.

Remarks. Taxonomic confusion exists regarding this genus. Although being the same genus, the names *Scombrinus*, *Auxides* and *Scombrosarda* are all frequently used as valid names. *Scombrinus speciosus* (Agassiz, 1835), is labelled as *Auxides propterygius* Agassiz, 1844, in the collections of the USNM and BMNH, but referred to as *Scombrosarda propterygia* in Bannikov & Sorbini (1984) and Bannikov (1985). *Auxides* is not mentioned in Bannikov & Sorbini (1984). Russian scientists consider *Auxides* as a synonym of *Scomber* (Bannikov, 1985; Danil'chenko, 1960). However, clearly discernible characters as the dorsal fins close together and a comparatively thick scale covering separates *Scombrinus* from *Scomber*. Moreover, the diagnoses of *Scombrinus* and *Scombrosarda* perfectly agree. *Scombrinus* Woodward, 1901 has age preference over both *Auxides* Jordan, 1919 and *Scombrosarda* Danil'chenko, 1962. Bannikov (1985) synonymised *Tamesichthys* Casier, 1966 with *Scombrosarda* and thus mentioned *Tamesichtys decipiens* Casier, 1966 as *Scombrosarda decipiens* (Casier, 1966). A reason why

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[5]In Ciobanu (1977) *Pinulothunnus* is mentioned as *nov. gen.*, although it was first described as a new genus in Ciobanu (1970).

Tamesichthys is recognised as a synonym for *Scombrosarda* is not given. The head of *Tamesichthys* is twice as long as deep, while the head of an *Scombrinus* is about as deep as long (measured in BMNH P15091). Also, the anterior margin of a *Tamesichthys* operculum is only slightly arched, while the preoperculum of *Scombrinus* is clearly crescent-shaped. Thus, *Tamesichthys* is not identical with *Scombrinus*.

"*Auxides dasson*" Jordan, 1921 is similair to *Auxides*, but possesses 35 vertebrae. I have not seen any specimens, so I cannot comment on the identity of the species. The name *Auxides dasson* reappeared as a junior synonym of *Scomber colias* Gmelin, 1789 (Arambourg, 1925 and 1927), which is in turn a synonym of *Scomber japonicus* Houttuyn, 1782.

Bannikov & Sorbini (1984) and Bannikov (1985) compared *Scombrinus* to *Grammatorcynus*. One of the differences between these genera they noted, is the presence of a lateral keel on the peduncle of the tail of *Grammatorcynus*, which is absent in *Scombrinus*. I assume the bony support for a fleshy caudal keel is meant, which is present in Thunnini and Sardini, but absent in other scombroids.

Scombrinus cernegurae (Ciobanu, 1970) comb. nov. (Fig. 7.20)

Pinulothunnus cernegurae Ciobanu, 1970: 83, pl. V, fig. 1. Type loc. Piatra Neamţ, Romania, Oligocene.

Scombrosarda limata Danil'chenko, 1980: 154, fig. 49, pl. XVIII. fig. 1. Type loc. river Belaya, Russia, Oligocene.

Scombrosarda cernegurae Bannikov & Sorbini, 1984: 309; Bannikov, 1985: 19, figs. 6-9, pl. II fig. 1. Type loc. *ibid.*

Diagnosis. Five dorsal and anal finlets, distance between first and second dorsal fin slightly more than half diameter of orbit, first caudal haemal spine bent into a sickle shape.

Referred specimens. PIN 3363-60, 3363-65, 3363-66, 3363-69, 3363-71, 3363-73, 3363-80, 3363-82, 3363-138, 3363-139 (Fig. 7.20b) and 3363-141 (Fig. 7.20a); river Belaya in Abadzekhskaya village, Caucasus, Russia, Early Oligocene: Rupelian (Pshekha Horizon), river Belaya in Abadzekhskaya village, Caucasus, Russia, Early Oligocene: Rupelian (Pshekha Horizon); PIN 3363-83, river Gumista, Bereg Province, Abkhazia, Georgia, Early Oligocene: Rupelian (Pshekha Horizon).

Description. Detailed description provided by Bannikov (1985). Additional observations and differences are indicated here. Lachrymal larger than diameter of orbit. Pterotic a short wing. Dentary with a dorsal and ventral process. Ventral margin of ceratohyal smooth, without projections. Gill filaments not modified with

denticles and interconnections. First dorsal fin contains X-XIII (X-XI according to Bannikov) spines. Second formula I+9-11 (I+11 according to Bannikov). Anal fin formula II+10-11 (II+11 according to Bannikov). Pectoral fins projecting slightly postero-dorsally, 14-17 rays (20-22 according to Bannikov). Pelvic fins longer than pelvic projection. Pelvic plate simple, consisting of one single wing. Caudal skeleton: fifth hypural and parhypural free. Procurrent spur absent. Tail fin hypurostegic, with 30-40 rays. Scale covering slightly increased in the shoulder girdle region, forming weak similarity to corselet.

Scombrinus devius (Danil'chenko, 1962) comb. nov. (Fig. 7.21)

Scombrosarda devia Danil'chenko, 1962: 122, fig. 10. Type loc. Tbilisi, Georgia, Eocene.

Diagnosis. Eight finlets (dorsal and anal), first haemal spine bent in sickle-shape.
Referred specimens. PIN 1413-79 (two counterparts, **holotype**, one counterpart Fig. 7.21). Tbilisi, Georgia, Middle Eocene (Dabakhansk Svita).
Description. Detailed description given by Bannikov (1985). I have counted eight pairs of finlets, while Bannikov reports seven.

Scombrinus speciosus (Agassiz, 1835a) comb. nov (Fig. 7.21).

Scomber pelamis Volta, 1796: 66, pl. XIV, fig. 2 (*non* Linnaeus, 1758). Type loc. Monte Bolca, Italy, Eocene.
Scomber trachurus Volta, 1796: 125, pl. XXIX, fig. 2[6] (*non* Linnaeus, 1758). Type loc. *ibid.*
Scomber speciosus Volta, 1796: 169, pl. XLI (*non* Forsskål, 1775). Type loc. *ibid.*
Ophicephalus striatus Volta, 1796: 193: pl. XLVIII, fig. 1 (*non* Bloch, 1793). Type loc. *ibid.*
Labrus bifasciatus Volta, 1796: 204, pl. L, fig. 1 (*non* Bloch, 1791). Type loc. *ibid.*
Scomber speciosus? De Blainville, 1818: 346.
Thynnus propterygius, Agassiz (1835a): 292 (*nomen nudum*)
Cybium speciosum Agassiz (1835a): 293. Type loc. *ibid.*
Thynnus propterygius Agassiz, 1833-44: 55, pl. 27. Type loc. *ibid.*
Auxis (?) propterygius, Woodward, 1901: 464. Type loc. *ibid.*
Scombrosarda propterygia Bannikov & Sorbini, 1984: 309, figs. 1-3, 6. Type loc. *ibid.*

Diagnosis. First haemal spine slightly bent (not with a sickle shape), seven or eight dorsal and ventral finlets.

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[6]Bannikov & Sorbini (1984) state that the name *Scomber triurus* has been erroneously given to this species. A reason is not given. I have nowhere found a reference to the epithet *triurus*. If it can be validated, the correct name for this species should become *Scombrinus triurus* (Volta, 1796).

Referred material BMNH P4136 & P1989 (counterparts), P4137, P4480 (two counterparts), P9942 (Fig. 7.22), P15091, P16302 and P16303, Monte Bolca, Italy; USNM 1946, Monte Bolca, Verona, Italy; Lutetian (Monte Bolca Formation).
Description. A detailed description of this species is given in Bannikov & Sorbini (1984), under the name *Scombrosarda propterygia.* The differences between their description and my observations are mentioned here. An adapted meristic formula is as follows. Vertebrae: 31 (13 precaudal), first dorsal: X-XII, second dorsal: I+8-13, anal: II+10-11, dorsal and anal finlets 7-8 pairs, pelvic I+5. The caudal complex is misrepresented in Bannikov & Sorbini (1984). Their unroneural is the fifth hypural and their stegural is the uroneural.
*Remarks.*This species is known under the epithet *propterygius*, in either genus *Auxides* or *Scombrosarda.* However, *Cybium speciosum* (see Agassiz, 1833-44) perfectly fits the diagnosis of *Sombrinus propterygius.* Some of the studied specimens (BMNH P4136, P1989 and P9942) are labelled as *Cybiun speciosum.* This epithet was for this species for the first time validly published as *Cybium speciosum* Agassiz, 1835 (*Scomber speciosus* Volta, 1796 and the other synonyms published by Volta are unavailable preoccupied names). Thus, the epithet *speciosus* has age preference over *propterygius*, which was, for this species, for the first time validly published as *Thynnus propterygius* Agassiz, 1844.

Scombrinus turkmenicus (Danil'chenko, 1968) comb. nov. (Fig. 7.23)

Scombrosarda turkmenica Danil'chenko, 1968: 151, pl. XXXIII, fig. 3, text-fig. 16. Type loc. Uilya-Kushlyuk, Turkmenistan, Eocene.

Diagnosis. Five or six pairs of finlets (anal or dorsal), first haemal spine not strongly bent.
Referred specimens. BMNH P1898, Tangi-Kora, Imam Hassan, Iran, Middle Eocene; PIN 2179-51 (**holotype**, Fig. 7.23), 1762-82, 2179-53, Uilya-Kushlyuk village, Turkmenistan, Ypresian, (Middle Danatinsk Svita).
Description. Detailed description give by Bannikov (1985). Additional information and differences noted here. Prenasal absent. Vertebra medially slightly constricted. Pectoral with 17-18 rays (19-21 in Bannikov, 1985). First dorsal with X spines (XIII *sensu* Bannikov). Second dorsal I+13, I+12-13 according to Bannikov. Anal fin I+13 (II+11-12 *sensu* Bannikov). Five or six finlets (anal or dorsal), Always six according to Bannikov. Caudal fin with 30 lepidotrichia.
Remarks. Previously, this species was known only from the Ypresian, Danatisk Svita of Turkmenistan (Bannikov, 1985). The new specimen of *S. turkmenicus* enlarges the age range of the species to the Middle Eocene and also enlarges its area beyond Turkmenistan, and into Iran.

Subfamily **Godsillinae** subfam. nov.

A new subfamily of fossil fishes, as far as now containing only one genus and species described below. The taxon in question is characterised by an anteroventral corselet of thickened and enlarged scales between pelvic and anal fins.

Genus ***Godsilla*** gen. nov.

Scomber Volta, 1796: cxxiii, pl. xxix, fig. 1 (*non* Linnaeus, 1758)

Salmo Volta, 1796: ccxiv, pl. lii (*non* Linnaeus, 1758).

Clupea De Blainville, 1818: 343 (*non* Linnaeus, 1758).

Orcynus Agassiz 1835: 293 (*non* Rafinesque-Schmaltz, 1815).

Thynnus Storms, 1889: 178 (*non* Cuvier, 1817).

Etymology. Named after the late H.C. Godsil, an expert of bonito- and tuna-like fishes.

Diagnosis. Dorsal and neural spines thick, pterygiophores wide, anteroventral corselet of enlarged and thickened spines. The only species of this genus was considered a *Thunnus* probably because of enlarged anterior scales, but it lacks *Thunnus* synapomorphies such as cephalic foramina, has much thicker neural and haemal spines, wider pterygiophores and less vertebrae.

Type species. Only one species, described below.

Species composition. Only the type species.

Godsilla lanceolata (Agassiz, 1835) comb. nov. (Fig. 7.24)

Scomber alatunga Volta, 1796: cxxiii, pl. xxix, fig. 1 (*non* Gmelin, 1789). Type loc. Monte Bolca, Italy, Eocene.

Scomber orcynus l.c.: cxxvi, pl. v, fig. 2. *ibid.*

Salmo cyprinoides Volta, 1796: ccxiv, pl. lii (*non* Linnaeus, 1766). Type loc. *ibid.*

Clupea cyprinoides De Blainville, 1818: 343. Type loc. *ibid.*

Orcynus lanceolatus Agassiz 1835: 293. Type loc. *ibid.*

Orcynus latior l.c.: 294. Type loc. *ibid.*

Thynnus lanceolatus Storms, 1899: 178. Type loc. *ibid.*

Diagnosis. As for genus.

Referred material. BMNH P3946, Monte Bolca, N. Italy, Lutetian (Monte Bolca Formation) (Fig. 7.24).

Description. Lachrymal small, shorter than diameter of orbit. Supratemporal groove short, not extending up to anterior tip of frontal. Frontoparietal fenestrae and pineal window absent. Teeth in single row, small, conical and straight.

Vertebrae 36 in number. Vertebrae slightly constricted medially, short (about 1.4 times as long as deep). Preural not suddenly shortened compared to preceding vertebrae. Tail fin hypurostegic. Median caudal fin rays enlarged and widely spaced. Dorsal fins drawn closely together. First dorsal spinous, exact number of spines not countable in specimen. A figure of what may be the holotype of *Orcynus lanceolatus* (Agassiz, 1833-44, pl. 23) shows XIII first dorsal spines. Second dorsal formula I+12. Anal fin with 10 or 11 soft rays, which may or may not be preceded by a spine. Thirteen dorsal and ventral finlets. Anteroventral corselet of thick and large scales present between head and pelvic fins and surrounding base of these. Some of these scales have pattern of concentric rings preserved, some of them are splint-like structures that overlap each other strongly. Rest of body covered by small scales.

Remarks. I have not seen the original description of *Orcynus latior*. Agassiz (1833-44) described *Orcynus latior* and included *Scomber orcynus* in its synonymy. A reason for rejecting the epithet *orcynus* is not given. As far as I can assess, *Scomber orcynus* is only referrable to the species in question. It may thus be that its name will have to be emended to *Godsilla orcyna* (Volta, 1796),

It is possible that the anteroventral corselet is larger in other specimens of this species. According to Agassiz (1833-44) *Orcynus lanceolatus* is covered by large scales, which are best distinguishable where they cover the abdominal cavity. Besides *Orcynus lanceolatus*, Agassiz (1833-44) described *Orcynus latior*. The latter species differs from *O. lanceolatus* only by a more stocky outline. Agassiz' figures (Agassiz 1833-44, pls. 23, 24) do not reveal any other differences. Here, I consider both species conspecific, with the epithet *lanceolatus* having page preference. *Godsilla* appears as the sister group of a clade consisting of *Palaeothunnus*, Scomberomorinae, Sardinae, *Acanthocybium*, *Eothynnus* and billfishes.

Subfamily **PALAEOTHUNNINAE** subfam. nov.

Monogeneric (and monospecific) subfamily of scombrids. The only genus, *Palaeothunnus*, is described below. *Palaeothunnus* is the primitive sister group of the Scombridae above the scombrins. *Palaeothunnus* has a more advanced hypural fusion pattern than scombrins and more vertebrae, but less vertebrae, and larger scales than in the basal taxa of the scombrids above *Palaeothunnus* (see also cladogram in Chapter 8).

Genus ***Palaeothunnus*** Bannikov, 1978

Palaeothunnus Bannikov, 1978: 48.

Diagnosis. Vertebrae 38 in number Hypurals 1-4 fused into one single plate with rudimentary caudal notch. Body covered by moderate sized scales which are slightly larger in anterior region.
Type species. *Palaeothunnus parvidentatus* Bannikov, 1978.
Species composition. Only the type species.
Remarks. With the present state of knowledge, it seems implausible that *Palaeothunnus* belongs to the Sardini or Thunnini. The body shape, the number of vertebrae and finlets and the absence of the caudal notch (which is actually present, but rudimentary) probably led to Bannikov's original diagnosis of a "Thunnidae". However, since the preural centra are not remarkably shortened, *Palaeothunnus* can be neither a Sardini nor a Thunnini. *Palaeothunnus* could however still be considered a sister taxon of a Sardini+Thunnini clade. The fact that the scales are enlarged in the anterior region (although not forming a clear corselet) and the caudal notch is almost closed could support this. The cladistic analysis will hopefully bring more insights in *Palaeothunnus* relationships.

Palaeothunnus parvidentatus Bannikov, 1978 (Fig. 7.25)

Palaeothunnus parvidentatus Bannikov, 1978: 48. Type. loc. Uilya-Kushlyuk, Turkmenistan, Eocene.

Diagnosis. As for genus.
Referred specimens. PIN 1762-86, 3363-20, (**holotype**, Fig. 7.25a), 3363-21, (**paratype**) and 3363-22 (Fig. 7.25b); Uilya-Kushlyuk village, Turkmenistan, Early Eocene: Ypresian (Lower Danatinsk Svita).
Description. Detailed description given by Bannikov (1985). Different observations and additional information given here. Supratemporal grooves short, not extending to anterior apex of frontal. postero-superior fossa beyond middle of orbit. Cranial crest extending to anterior end of braincase. Pterotic spine short. No posterior intercalary projection. Thirty-eight vertebrae counted (40 according to Bannikov). There is, seemingly, suture that separates hypural plate into two small plates. However, this suture seems to me a rather shallow groove. Hence, I consider hypural plate consisting of fused hypurals 1-4, with rudimentary caudal notch (absent according to Bannikov). It is not clear whether fifth hypural is completely or partially fused to plate, nor is it clear if uroneural and urostyle are also fused to form part of hypural plate. Thirty-four hypurostegic caudal fin rays. Median caudal fin rays enlarged and widely spaced. Procurrent spur absent. Pelvic fin I spine and 5 soft rays. First dorsal inserted in third interneural space. Thirteen first dorsal fins

(XIV-XVI according to Bannikov), Not sure if there is a spine preceding soft rays in second dorsal. I counted 17 soft dorsal fins. Bannikov reported I spine followed by 14-15 rayas. Twelve dorsal finlets, 11 ventral (possibly 10 according to Bannikov). Pectoral fin with 13-17 (17-19, according to Bannikov) rays. Body covered by moderate sized scales, which are slightly larger in cranial region, but not forming clear corselet.

Subfamily SCOMBEROMORINAE Starks, 1910

Genus *Scomberomorus* Lacépède, 1802

Scomber Bloch, 1793: 38 (*non* Linnaeus, 1758).

Scomberomorus Lacépède, 1802: 292.

Polipturus Rafinesque-Schmaltz, 1815: 84.

Cybium Cuvier, 1817: 120.

Apolectus Bennett, 1831: 146.

Apodontis Bennett, 1832: 169.

Chriomitra Lockington, 1879: 133.

Sierra Fowler, 1905: 766.

Sawara Jordan & Hubbs, 1925: 214.

Pseudosawara Munro, 1943: 68.

Indocybium Munro, *l.c.*: 68.

Diagnosis. Caudal complex: fusion of urostyle and hypurals 1-5 (hypural 5 partially). Vertebrae 41-56 in number, anterior margin of vomer spatulate and strongly protruding, anterior margin of ethmoid emarginated, body covered by moderate sized scales. Differs from *Acanthocybium*, which has more vertebrae, more tightly packed and blunt-tipped teeth, a spatulate vomer which protrudes less strongly, and a large mid-lateral dent in vertebrae. *Scomberodon* and *Palaeocybium* also have blunt-tipped and tightly packed teeth. Differs from *Grammatorcynus* which has only 32 vertebrae and anterior margin of vomer that scarcely protrudes.
Type species. *Scomberomorus regalis* (Bloch, 1793) (Recent).

Species composition. Eighteen Recent species are known, found in tropical and subtropical coastal seas. Twelve fossil species are recognised here, found from the Palaeocene to the Miocene, is sediments from Western Europe, Congo-Kinshasa, Southwestern Russia and Turkmenistan. Bannikov (1985) lists all fossil *Scomberomorus* known to that date. That list has changed here, in that I question the validity of both *Scomberomorus bartonensis* (Woodward, 1901) and *Scomberomorus excelsus* (Woodward, 1901), recognise *Scomberomorus speciosus* as a *Scombrinus* (see description of *Scombrinnus speciosus*) and reinstate the validity of *Scomberodon dumonti*, rather than considering it part of

Scomberomorus. *Scomberomorus avitus* Bannikov, 1985; *Scomberomorus saevus* Bannikov, 1982 and supposed *S. excelsus/S. bartonensis* are described below and a few specimens of *Scomberomorus* whose specific identity could not be verified are mentioned.

Scomberomorus avitus Bannikov, 1985 (Fig. 7.26)

Scomberomorus avitus Bannikov, 1985: text-fig. 15, pl. III, fig. 4; pl. IV, fig. 1. Type loc. Uilya-Kushlyuk, Turkmenistan, Eocene.

Diagnosis. Thirteen anal fin rays. Recent *Scomberomorus* have 15-25 anal fin rays.

Referred specimens. PIN 1762-86 (**holotype**) and 1762-87 (**paratype**), Uilya-Kushlyuk village, Turkmenistan, Early Eocene (Ypresian, Middle Danatinsk Svita).

Description. Detailed description given by Bannikov (1985). In that description, six pairs of finlets recorded. Only four preserved, so number of six is (hazardous) estimate.

Remarks. The specimens described as *S. avitus* surely do not belong to Recent *Scomberomorus*, which clearly have less anal fin rays. Comparisons between *S. avitus* and other fossil *Scomberomorus* are made on the basis of characters such as the shape of the teeth, the premaxilla and the dentary. The dentary of *S. avitus* (Fig. 7.26) seems significantly deeper than that of *S. saevus* (see Bannikov, 1985, figs. 15, 16). I am uncertain, however, of the characters used to distinguish between the other species. I have not seen many species of fossil *Scomberomorus* of which the jaws are well enough preserved for comparison, and have not seen their descriptions either. I accept here the validity of *S. avitus*, but admit that this validity could be overturned by comparison with more specimens.

Scomberomorus saevus Bannikov, 1982 (Fig. 7.27)

Scomberomorus saevus Bannikov, 1982: 143, fig. 1. Type loc. Mangyshlak, Kazakhstan, Eocene.

Diagnosis. Angle between ascending process of premaxilla and its posterior shank 37°, 26 teeth in premaxilla, estimated forklength 2800 mm. Differs from *Scomberomorus lineolatus* (Cuvier, 1831) which has premaxilla with approximately same anterior angle (32-36°, Collette & Russo, 1984) in body size: *S. lineolatus* has maximum forklength of 800 mm (Collette & Russo, 1984).

Referred material. PIN 1878-3, 1878-8 (**holotype** Fig. 7.27) and 1878-9, Mangyshlak peninsula, Karagiye basin, Kazakhstan, Late Eocene: Priabonian (Shorym Svita).

Description. Detailed descriptions given by Bannikov (1982, 1985). The original description from 1982 in Russian is also available in an English translation. Different observations and additional information given here. Exact dimensions of premaxilla difficult to measure. My measurements do not seem to differ significantly from those of Bannikov. Angle between ascending process and posterior shank 37° (~35° according to Bannikov); ascending process covers ~50% of total length of premaxilla (45-47% *sensu* Bannikov). Also, number of premaxillary teeth difficult to assess due to damage. While I believe this number to be 26, Bannikov suspected it is between 26 and 29.

Remarks. Part of the type series of *S. saevus* (two hypural plates) do not belong to *Scomberomorus*. PIN 1878-2 is described below, together with fossils found in the U.S.A. as *cf. Acanthocybium*.; PIN 1878-4 is described below, together with a fossil found in London Clay sediments, as *Gymnosarda prisca* Monsch, 2000.

The number of teeth in the premaxilla was thought to be significantly more than in Recent *Scomberomorus*. While Bannikov reported the number of premaxillary teeth in Recent *Scomberomorus* to be 22, Collette & Russo (1984) showed that in *Scomberomorus* the number of teeth per premaxilla varies between 5 and 39. Bannikov (1985) indicated that the estimated forklength of *S. saevus* is 2800 mm. It is not indicated how this estimate was made, but I assume that the size of the individual bones were compared to those in other (Recent?) *Scomberomorus* in relation to their respective forklengths, and that based on these comparisons an extrapolation was made to estimate a length of 2800 mm. I believe that these figures should be processed with care, considering possible heterochrony between different species. However, it is clear that *S. saevus* was a large fish. The largest *Scomberomorus* specimen I have observed is a 1850 mm *Scomberomorus sinensis*. Collette & Russo (1984) report that *Scomberomorus commerson* can reach up to 2300 mm forklength. *S. saevus* differs from other fossil *Scomberomorus* mainly in dental characters. Most of those fossil species are unknown to me. I accept the validity of *S. saevus*, unless comparison with specimens (or descriptions) of other species will prove otherwise.

Scomberomorus sp. 1 (Fig. 7.28)

Cybium excelsum Woodward, 1901: 567, fig. 15. Type loc. Hampshire, England, Eocene.

Cybium bartonense Woodward, 1901: 567, fig. 16. Type loc. Barton, England, Eocene.

Scomberomorus bartonensis Bannikov, 1985: 34. Type loc. *cf. C. bartonensis.*

Scomberomorus excelsus Bannikov, 1985: 34. Type loc. *cf. C. excelsum.*

Diagnosis. Ascending process of premaxilla makes angle of approximately 40° with posterior shank.

Referred specimens. BMNH 1193, P14029 (some material of this number is mentioned under *Acanthocybium* and *Scomberodon*), Barton, England; P53, (**holotype** of *Cybium bartonense*, Figs. 7.28a, c), near Christchurch, Hampshire, England; P1528 (**holotype** of *Cybium excelsum*), P3958 (Fig. 7.28b), Barton Cliff, Hampshire, England. All fossils of Bartonian age (Barton Clay).

Description. Short descriptions of both "*Cybium bartonense*" and "*Cybium excelsum*" are given by Woodward (1901). Anterior ascending process of premaxilla makes angle of approximately 40° with posterior shank. Vertebrae deeper than long, and in cross-section wider than deep, with deep lateral dents.

Remarks. Woodward (1901) described the material discussed here under two different names: *Cybium bartonense* and *Cybium excelsum.* However, I have come to believe that the fossils described under either name are conspecific. The angle between the ascending process and shank of the premaxillae is approximately the same in both *C. bartonense* and *C. excelsum.* According to Woodward, the most anterior premaxillary teeth of *C. excelsum* scarcely differ in size from those in the dentary, while in *C. bartonense* the anterior premaxillary teeth are clearly smaller than those of the dentary. I however failed to see a significant difference between the two supposed species in this respect. The most anterior teeth in the premaxilla of *Scomberomorus* always seem smaller than the subsequent ones and smaller than the anterior mandibular teeth. This seems to be the case in both "*C. excelsum*" and "*C. bartonense*", without a difference sharp enough to warrant a specific division. I failed to discover differences in other characters, such as those of the dentition or the morphology of the dentary, that are significant enough to distinguish between two species. Woodward (1901) seemed to base his diagnosis of the species of *Cybium* he described on differences between the fossil specimens, but made no reference to Recent *Scomberomorus*. Collette & Russo (1984) mentioned a group of four species (*Scomberomorus cavalla* (Cuvier, 1829), *Scomberomorus commerson* (Lacépède, 1800), *Scomberomorus maculatus* (Mitchill, 1815) and *Scomberomorus regalis* (Bloch, 1793)) that have premaxillae with angles of 41-54° between the ascending process and the posterior shank. The fossils described as *C. bartonense* and *C. excelsum* fall into that category. On the basis of the fragmentary material it is difficult to estimate the size a complete specimen of these fossils would have had. Of the Recent species of the "41-54°-group", only two species could approach the possible size of the fossils. I have seen specimens of *S. cavalla* of up to 920 mm forklength and of *S. commerson* of

up to 1155 mm forklength. However, Collette & Russo (1984) mention of only six of the 18 species of Recent *Scomberomorus* the angle between ascending process and shank. The fossil material is fragmentary and does not seem to have useful specific apomorphies preserved. Hence, these fossils are potentially referable to many different species of Recent *Scomberomorus* (hereby supposing a considerable longevity). There are other large *Scomberomorus* known, such as the large specimen (1850 mm forklength) of *Scomberomorus sinensis* (Lacépède, 1800) that I studied. The fossils might, alternatively, belong to any other fossil species of *Scomberomorus*. If they belong to a species in their own right, their correct name is *Scomberomorus excelsus*. Both *Cybium excelsum* and *Cybium bartonense* appear on page 476 in Woodward (1901), with *C. excelsum* mentioned earlier on the page.

***Scomberomorus* sp. 2** (Fig. 7.29)

Diagnosis. Scomberomorus-characters: diameter of caudal vertebrae oval with the long side horizontal; caudal neural and haemal spines very robust; caudal centrums on each side with a pair of deep, sharply boundered dents, hypural plate consists of urostyle, uroneural and hypurals 1-4 (and 5 partially). Parhypural autogenous.
Referred material. BMNH P6207, Malta, Early Miocene (Burdigalian-Landinian, vertebrate beds of *Globigerina* Limestone, dates according to Steininger (1985).
Description. Scomberomorus: caudal vertebrae longer than in Sardini, shorter than in Scombrinae (*Scomber*, *Rastrelliger*). Preural 5: 27 mm long, 21 mm deep; diameter of caudal end: 22 mm wide, 17 mm deep; caudal neural and haemal spines very robust; caudal centrums on each side with a pair of deep, sharply boundered dents. Hypural plate damaged. Consists of urostyle, uroneural and hypurals 1-4. Hypural 5 not preserved in this specimen but most likely to be partially fused to plate. Dorsal process of uroneural rather large and slender. Parhypural loose, with large anterodorsal process (damaged).
Remarks. There are no diagnostic features in the specimen that make it possible to identify the species. The size of the specimen does not clarify its specific status either. Modern *Scomberomorus* are measured with lenghts of 272-1590 mm. The maximum length recorded however, is 2200 mm, for *Scomberomorus commerson* (Collette & Nauen, 1983). A 456 mm long *Scomberomorus regalis* (USNM 270055) has a hypural plate of 30 mm deep. Its lower half is 12.7 mm. The lower half of the hypural plate of BMNH P6207 is damaged but is estimated to 32 mm. Extrapolating the data of this *S. regalis* to BMNH P6207, it could have achieved a length of 1149 mm.

Gen. et sp. **indet.** (Fig. 7.30)

Diagnosis. Hypurals 1-4 and urostyle fused into plate.
Referred material. BMNH P1530 (Fig. 7.30), Isle of Wight, Lutetian (Bracklesham Beds).
Description. Hypural plates and vertebral remains. Hypurals 1-4 and urostyle fused. Position of hypural 5 uncertain. Caudal notch present. Plate diamond-shaped, sides about equal in length and distal margins slightly swollen. Superficial grooves indicate that plate was (almost) completely covered by caudal fin lepidotrichia. Urostyle wider than deep. Uroneural and parhypural autogenous. Vertebrae short and robust, with stout neural and hamal spines. Much detail of centra obscured by matrix.
Remarks. The fusion of hypurals into one solid plate is a synapomorphy of Scomberomorinae and scombrids above them. In other scombrids, the condition is more derived in that uroneural and parhypural may be fused into the plate and that caudal notch may disappear. Within the Scomberomorinae, BMNH P1530 resembles most *Scomberomorus*, whose vertebrae are aslo short, as opposed to *Grammatorcynus* which has vertebrae which are longer than deep. It is not clear to me however, if long vertebrae are plesiomorphous or apomorphous, hence I cannot, for the moment, determine a more exact systematic status of these fossils. Moreover, in *Scomberomorus* the hypural plate tends to be more triangular rather than diamond-shaped.

Subfamily **SARDINAE** Starks, 1910

Tribe **Sardini** Starks, 1910

Genus *Gymnosarda* Gill, 1862

Thynnus (*Pelamis*) Rüppell

835-38): 40, pl. 12, fig. 1 (*non* Cuvier, 1817).

Pelamys Günther, 1860: 368 (*non* Cuvier, 1832).

Gymnosarda

Scomberomorus Bannikov, 1982: 135 (*pro parte*); Bannikov 1985: 37 (*pro parte*) (*non* Lacépède, 1801).

Diagnosis. A genus of Sardini characterised by a parhypural that is fused to the hypural plate and a tendency of the caudal hypural notch to close.
Type species. *Gymnosarda unicolor* (Recent).
Species composition. There is only one Recent species known: *G. unicolor*. Below, an unidentified *Gymnosarda* from the London Clay is mentioned, as well as *Gymnosarda prisca* Monsch, 2000. The systematic palaeontology of *G. prisca* is

taken from Monsch (2000), with only slight modifications. *Gymnosarda* fossils are found in the Eocene and Oligocene of Europe.

Gymnosarda prisca Monsch, 2000.(Fig. 7.31)

Scomberomorus saevus Bannikov, 1982: 135 (*pro parte*); Bannikov 1985: 37 (*pro parte*).

Holotype. BMNH P6485, Sheppey, England, Early Eocene: Ypresian (London Clay) (Fig. 7.31a).

Referred material. Holotype, and PIN 1878-4, Mangyshlak peninsula, Kazakhstan (Monsch, 2000 mistakenly states that the specimen originates from Turkmenistan in the Caucasus), Late Eocene: Priabonian (Shorym Svita) (Fig. 7.31b).

Etymology. Priscus is Latin for "old", indicating it is an extinct ancient species of *Gymnosarda*. The only Recent species is the *Gymnosarda unicolor.*

Diagnosis. Species of a Sardini: uroneural and fifth hypural fused to hypural plate and urostyle cross-section with long axis horizontal. Differs from other Sardini by having parhypural fused to hypural plate and possession of caudal notch. Recent bonitos lack a conspicuous notch, and of Recent bonitos only *Gymnosarda unicolor* has a fused parhypural (see Fig. 7.31c).

Description. Hypural plate, made up of fusion of urostyle, uroneural, hypurals 1-5 (hypural 5 not completely fused to plate) and parhypural. Plate diamond-shaped; sides equal in length. Height 75 mm (holotype, Fig. 7.31) or 79 mm (PIN 1878-4, Fig. 7.31b), which is twice the length without uroneural in both specimens (length: along axis of fish, height: along line perpendicular to axis). Posterior outline of diamond slightly swollen outwardly (more on dorsal side). Posteriorly, a clearly discernible notch. Markings made by fin rays crossing plate visible as shallow grooves, running parallel to rostral sides of diamond. Parhypurapophysis (damaged) making angle of about 41° with horizontal axis. Uroneural large, fused to urostyle (urostyle, according to definition of Potthoff (1975): fusion of preural centrum 1 and ural centrum). Cross-section of urostyle round or slightly ovoid with the long axis vertical (as Thunnini, Fig. 7.32a).

Remarks. The Russian specimen mentioned above belongs to the type series of *Scomberomorus saevus*. Bannikov (1982) did not describe hypural plates in the original description of *S. saevus*, although the type material did include these plates (Bannikov pers. comm., 1998). They are described in a later account (Bannikov, 1985). These hypural elements are part of a series of paratypes. The holotype of *S. saevus* is a premaxilla. Previously, *G. prisca* was believed to belong to *Scomberomorus* because of apparent similarities with the latter (Fig. 7.31). It now seems that it is not a *Scomberomorus*. The most conspicuous character to identify a Sardinae from a Scomberomorinae is the cross-section of their urostyles (see their descriptions and Fig. 7.32).*Gymnosarda prisca* has a hypural plate in which

the cross-section of the urostyle is ovoid with the long axis vertical (Fig. 7.32a), whereas in Scomberomorinae the long axis is horizontal (Fig. 7.32b). In *G. prisca* the parhypural is fused with the hypural plate, whereas in Recent *Scomberomorus* it is not. Collette and Russo (1984) mention that *Scomberomorus niphonius* (Cuvier, 1831) and *Scomberomorus plurilineatus* (Fourmanoir, 1966) have parhypurals partially fused to the hypural plate. In specimens of *S. plurilineatus* (USNM 264809 and 269760) and *Scomberomorus niphonius* (BMNH 1874.1.16.9 and 1890.2.26.90) the parhypural is not fused to the hypural plate. Possibly there is a light degree of fusion in specimens that I have not seen. Bannikov (1982) noted that the parhypural of *S. saevus* is separated from the hypural plate by a fissure. Although the parhypural can be clearly identified in the hypural plate of *G. prisca*, the division between the plate and the parhypural is not sharp enough to represent an autogenous parhypural.

The assignment of the name *S. saevus* to its whole type series is partially incorrect. Bannikov's (1982, 1985) holotype is PIN 1878-8, which is a premaxilla that is identical to one of *Scomberomorus*. A *Scomberomorus* premaxilla is recognised by a relatively long ascending process: 31-48 % of the total premaxilla, and makes a sharp angle with the shank: 32°-61° (Collette & Russo, 1984). The holotype of *S. saevus* fits this description well. Being recognised as a *Scomberomorus* and being the holotype of the epithet *saevus*, the name *Scomberomorus saevus* is retained for this specimen.

The hypural plate-based taxon *G. prisca* is referable to the Sardini based on the diamond-shaped plate and the large anterior upturned end of the uroneural which is fused to the plate. With its proportions the hypural plate of *G. prisca* is almost identical to that of the Recent *G. unicolor* (Fig. 7.31c). In *Gymnosarda*, the hypural plate is about twice as deep as long. In the other bonitos *Sarda*, *Orcynopsis* and *Cybiosarda* the hypural plate is less deep. *Allothunnus* was previously recognised as a bonito (Collette & Chao, 1975; Johnson, 1986). Collette *et al.* (1984) suggest that *Allothunnus* is better regarded as a primitive Thunnini, for which later convincing evidence has been found (Graham and Dickson, 2000). *Gymnosarda unicolor* is unique among Recent bonitos in having a fused parhypural, just like *G. prisca*, and has a small vestige where *G. prisca* has a caudal notch (BMNH 1934.3.31 and Collette & Chao, 1975, p. 578 and fig. 56). No bonito with a caudal notch is known (Collette & Chao, 1975). I have not seen such notches in specimens of *Sarda* (BMNH 1920.7.23.59; USNM 26953, 26954, 270730 and 270731). Still, the *G. prisca* hypural plate possesses all other characteristics of a Sardini.

The specimen figured in Fig. 7.32b (PIN 1878-2) is an unknown scombrid, described and figured as *S. saevus* by Bannikov (1985, p. 37, figures 17 g, d) and is part of the *S. saevus* type series. The parhypural is fused to the plate and hence it

is not a *Scomberomorus* (Table. 7.1), but no name as yet is assigned to that specimen. The systematic position of the taxon this plate represents is still under consideration.

Gymnosarda prisca shows a peculiar mix of characters. A noticeable caudal notch in the hypural plate is a primitive character, found in amongst others the Scomberomorinae, where it can be large. I do not think that G. *prisca* can be anything but a Sardini and indeed, a *Gymnosarda*. According to Collette and Chao (1975) and Collette *et al.* (1984) one of the synapomorphies of the scombrids above the Spanish mackerels (Scomberomorinae) is the absence of the caudal notch (see Table. 7.1). *Gymnosarda prisca* clearly possesses a large caudal notch. *Gymnosarda unicolor* is in fact not devoid of a caudal notch, it has a small, hard to spot vestigial one. It seems thus, that Sardini are not characterised by the absence of a caudal notch, but rather by a tendency of this notch to close down, and ultimately disappear in their evolution. Thunnini are characterised by a complete absence of the notch. The caudal notch in *G. prisca* is evidence that it is not a sharp divider above species level: the Scomberomorinae have a notch; so do primitive Sardini and in advanced ones this notch has disappeared. Therefore, because of the

Table 7.1 (from Monsch, 2000). Overview of hypural plate characters of *Scomberomorus* and Sardini.

	Parhypural	Caudal notch	Uroneural	Hypural fusion pattern	Urostyle
Scomberomorus	not fused	yes	not fused	1-4, 5	deeper than wide
G. prisca	fused	yes	fused	1-5	wider than deep
G. unicolor	fused	remnant	fused	1-5	wider than deep
other Sardini	not fused	no	not fused	1-5	wider than deep

great similarities with *G. unicolor*, I describe this fossil taxon as a new species within this genus.

The small vestigial notch of *G. unicolor* suggests that more primitive bonitos have once had a large caudal notch. This is confirmed by *G. prisca*. This notch is a primitive feature, which thus suggests that the ancestor of the bonitos came from within the Scomberomorinae (see Table 7.1).

In Collette *et al.*'s (1984) phylogeny, Sardini and Thunnini are the most advanced scombroids, with Scomberomorinae as the sistergroup (Fig. 7.33a). According to Johnson (1986), Sardini+Thunnini are a specialised offshoot of a paraphyletic Scomberomorinae (Fig. 7.33b). Finnerty and Block (1995) present a phylogenetic relationship in which the Sardini+Thunnini clade is sister-group to a

Scombrinae (mackerels)+Trichiurinae (cutlassfishes) clade (Fig. 7.33c). The clade containing these four taxa is in turn the advanced sistergroup to Scomberomorinae. Keeping in mind the proposed evolutionary sequence (Fig. 7.33d), all three hypotheses of relationships in Fig. 7.33 seem to be possible. Finnerty and Block's hypothesis is less parsimonious than the morphological ones, because it requires reversals. The caudal region of Scombrinae and Trichiurinae is plesiomorphous compared to that of other Scombridae. Johnson's (1986) Scomberomorinae are paraphyletic, caused by the offshoot of Sardini and Thunnini, but his phylogenetic hypothesis remains possible. However, this hypothesis is less parsimonious than that of Collette *et al.* (1984). If you map tail-region morphology on Johnson's (1986) phylogeny, there are character reversals (Fig. 7.33b). Further research on the phylogeny of scombroids will hopefully contribute more to the solution of the controversy of these relationships.

Although based on a hypural plate only, I do think that phylogenetic hypotheses can be made using *G. prisca*. Hypural plates provide strong characters, which are well indicative of genera (see Uyeno and Fuji, 1975).

***Gymnosarda* sp.** (Fig. 7.34)

Referred material. BMNH P1773b (Fig. 7.34a), Sheppey, England, Early Eocene: Ypresian (London Clay) Ypresian; P7537 (in part), Malta, Early Miocene (Burdigalian-Landinian, vertebrate beds of *Globigerina* Limestone) (Fig. 7.34b).

Description. This concerns two specimens which can be identified as *Gymnosarda*, but whose specific identity is uncertain. BMNH P1773b has a clearly more acute outline than the hypural plates of *G.prisca* and the centrum of its hypural plate also has a more laterally compressed diameter. Presence of caudal notch not absolutely certain since the specimen is damaged, but likely to have been present and of small size. Height of plate uncertain because of damage to the specimen. Height of dorsal half 38 mm. BMNH P7537 is the caudal part of the vertebral column and part of the caudal skeleton. Preural vertebrae 2-4 remarkably shortened, but not as strongly as in Thunnini. Urostyle deeper than wide, parhypural fused. Shape of hypural plate and size of hypural notch unknown.

Remarks. Another specimen which is also stored under collection number BMNH P7537 is not a scombroid fish. This interesting discovery will be described at a later date.

cf Gymnosarda **sp.** (Fig. 7.35)

Diagnosis. Deep dentary with symphysial chin-like process, large, ovoid, striated teeth. Large individual: distance between symphysis of dentary and 14th tooth 108 mm. Hypural plate with hypurals 1-4 and parhypural fused and urostyle cross-section deeper than wide.

Referred material. One damaged dentary, BMNH P4546 (Fig. 7.35), Sheppey, England, Early Eocene: Ypresian (London Clay); hypural plate BMNH 40278 (a), Brooks, Brooks, Hampshire, England, Late Palaeocene-Early Eocene: Thanetian-Ypresian (Reading and Woolwich Formations).

Description. Dentary: with large symphysial chin-like process. Deep, like dentary of *Sarda sarda*, in which d(symphysis-tooth 9)=65 mm and depth at tooth 10=42 mm. Consisting of two branches: a dorsal dentigerous branch and a ventral branch. Dentigerous part of dentary almost complete. Dorsal and ventral branch separating at the tenth tooth. Teeth conical, ovoid, straight or slightly curved inwards, slightly striated. All teeth damaged but probably have reached sizes of 6-6.5 mm, irregularly spaced. Distance between symphysis of dentary and 14th tooth 108 mm.

Hypural plate: much damaged specimen. Hypurals 1-4 and urostyle fused. Parhypural fused to plate. Hypural 5 and uroneural not preserved.

Remarks. Scombroid taxa possessing a large symphysial chin-like process are Sardini (with the best developed process in *Sarda*), *Eocoelopoma*, *Scomberomorus* and *Sphyraenodus*. BMNH P4546 was catalogued as *Sphyraenodus*. However, the dentary of *S. sheppeyensis* is clearly deeper than those most chin-bearing taxa except *Sarda*. *Scomberomorus* teeth are laterally somewhat compressed, while these teeth seem fully conical. BMNH P4546 perfectly fits diagnosis of Sardini, especially *Sarda sarda* or *Gymnosarda* because of the large "chin" and the deep dentary. The largest *Sarda* known today is *Sarda chiliensis chiliensis* Cuvier, 1831: ≤672 mm (Collette & Chao, 1975). BMNH P4546 measures 108 mm from the anterior symphysis to tooth no. 14. The length of the snout of *Sarda sarda*, is 9.3 % of total length of fish. Extrapolatinng these figures, one can estimate the fork length of the complete individual from which the dentary originates at just under 1000 mm. Fossil *Sarda* of former USSR are at most 800 mm long (Bannikov, 1985). *Gymnosarda* is the largest Sardini known to date. BMNH 1934.3.31 (*G. unicolor*) has a forklength of 860 mm., but specimens have been reported to reach lengths up to 1040 mm. I feel that it is not possible to conclude whether BMNH P4546 is an (undescribed?) *Gymnosarda* or a new, large species of *Sarda*. Estimated lengths of complete individuals based on size of a sbony element cannot be used as a definite morphometric characteristic. A new species of *Gymnosarda*, *G. prisca* was described from sediments in Kazakhstan and the London Clay

sediments from Sheppey (Monsch, 2000). It is possible that the dentary described here and the hypural plate of *G. prisca* belong together. However, I do not know if both the jaw bone and the English specimen of *G. prisca* are found together or in association. Until similar fossil specimens are found together, it is better to not definitely assign a name to BMNH P4546.

Due to the fragmentary nature of the hypural plate, it cannot be said with certainty whether it belongs to a *Gymnosarda*, even though the preserved characters agree with the diagnosis of that genus.

Genus *Sarda* Cuvier, 1829

Scomber Bloch, 1793: 44 (*non* Linnaeus, 1758).

Thynnus Risso, 1826: 415 (*non* Cuvier, 1817).

Sarda Cuvier, 1829: 199.

Pelamys Cuvier in Cuvier & Valenciennes, 1832: 149.

Palamita Bonaparte, 1831: 173.

Creotroctes Gistel, 1848: x.

Thunnus Danil'chenko, 1960: 156 (*pro parte*), pl. XVI, fig. 3.

Diagnosis. Most species with toothless vomer. Differs from other Sardini in more vertebrae (39-52) than *Gymnosarda* and *Orcynopsis* (38). *Cybiosarda* has 47 vertebrae (Collette & Chao, 1975) but differs from *Sarda* by added apomorphy of two tooth patches fused to basihya, compared to none in *Sarda*. *Sarda* differs from all other Sardini by more first dorsal spines (XVII-XXI) than in other Sardini, which have between XII and XVII (Collette & Chao, 1975).

Type species. *Sarda sarda* (Bloch, 1793).

Species composition. There afre five recent species (see Collette & Chao, 1975). Bannikov (1985) reports six fossil species, occurring in the Oligocene and Miocene in Russia, Algeria and California. The Californian species is *Sarda stockii* David, 1943 Based on meristic counts and a body depth greater than in known *Sarda*, David (1943) established this as a separate species of *Sarda*. However, updated meristic counts (Collette & Chao, 1975) prove that *S. stockii* is identical to *S. chiliensis*, and its location (California) is evidence that it belongs to the Northeast Pacific subspecies of *S. chiliensis*: *Sarda chiliensis* ssp. *lineolata* Girard, 1858. The fossil Russian species and a new *Sarda* from the Ypresian of England are described below. The Russian specimens described below could be diagnosed as Sardini based on the morphology of their teeth (moderatly stout and slightly curved elongated cones) and the caudal region preural vertebrae slightly less abruptly shortened, diamond-shaped single hypural plate) conforms with that of Sardini. Within the Sardini, *Sarda* is the only genus possessing a full scale covering, as is

also observed in the Russian specimens. Some meristic counts of these species however are novel and do not conform to those of Recent species (Collette & Chao, 1975). The ranges of the meristic values of *Sarda* are expanded by including the fossil species, but the differences with other Sardini remain clear. The Russian and English species known up to date are described below, as well as a new species from the London Clay sediments.

Sarda memorabilis Danil'chenko, 1980 (Fig. 7.36)

Sarda memorabilis Danil'chenko, 1980: 159, pl. XVIII, fig. 4. Type loc. Otradnaya, Russia, Miocene.

Diagnosis. Thirty-nine vertebrae, which is less than all other Sardini (*S. remota* has the next least number of vertebrae in *Sarda*, 41).

Referred material. PIN 3363-92, Urup River, Otradnaya village, Caucasus, Sakaraul'skii regional yarus, Russia, Early Miocene (Karadzhalgin Svita), PIN 3363-91 (**holotype**, Fig. 7.36b), Caucasus, Azerbaijan, Early Miocene (Zuramakent Horizon), PIN 1413-99 (Fig. 7.36a), North Osetiya, river Chyorna, Russia, Early Miocene (Assinskaya Svita).

Description. Specimens small: 41 mm (PIN 1413-99) or 38 mm (PIN 3363-91), Vertebral column with 39 (40 according to Bannikov) vertebrae. Three preural vertebrae visibly shortened. Hypural plate consisting of hypurals 1-5 (hypural 5 partially fused to plate), no caudal notch, parhypural autogenous, parhypurapophysis with concave anterior margin. Caudal fin deeply forked, with 27 (PIN 1413-99) or 32 (PIN 3363-91) rays, deeply overlapping hypural plate, no procurrent spur. Pelvic plate large, with clearly differentiated wings. Interpelvic process shorter than pelvic fin. Pelvic fin small, with 1 spine and 5 soft rays. Pectoral fin with 15 (16-18, according to Bannikov) rays, First dorsal fin with XVII (XV according to Bannikov) spines, Second dorsal fin with 12 (up to 13 *sensu* Bannikov) soft rays. Six (Seven according to Bannikov) anal and dorsal finlets.

Sarda rara Bannikov, 1979 (Fig. 7.37)

Thunnus abchasicus Danil'chenko, 1960: 149 (*pro parte*) , pl. XVI, fig. 3. Type loc. North Osetiya, Russia, Oligocene.

Sarda rara Bannikov, 1979: 98, fig. 1. Type loc. river Belaya, Russia, Oligocene.

Diagnosis. Forty-one vertebrae (less than in Recent *Sarda*, which have at least 43 vertebrae), 15 soft elements in the second dorsal fins.

Referred specimens. PIN 3363-18, (**holotype**, Fig. 7.37a), river Belaya in Abadzekhskaya village, Caucasus, Russia, Early Oligocene: Rupelian (Pshekha Svita) and PIN 483-2 (Fig. 7.37b, c), North Osetiya, Russia, Early Oligocene: Rupelian (Lower Khadum Horizon).

Description. Detailed description given in Bannikov (1985). Different observations and additional information given here. Total body length 75 mm (holotype). Pterotic a short wing. Vertebral column with 41 (or possibly 40, according to Bannikov) vertebrae. Incomplete bony caudal keel present (Fig. 7.37c). Caudal fin deeply forked, with 58 rays (PIN 483-2), deeply overlapping hypural plate, no procurrent spur. Pelvic girdle not well preserved. Pectoral fin with 23 (28 according to Bannikov) rays, pointing slightly dorso-caudad. First dorsal fin with XVII (XVI according to Bannikov) spines, much less deep than body. Second dorsal fin with I+15 (possibly 14 according to Bannikov) rays.

Sarda remota Danil'chenko, 1960 (Fig. 7.38)

Scomber voitesii Danil'chenko, 1960: 152 (*pro parte non* Paucă, 1929) pl. XXII, fig. 1. Type loc. river Gumista, Georgia, Oligocene.

Sarda remota Danil'chenko, 1980: 158, fig. 51, pl. XVIII, fig. 3. Type loc. river Belaya, Russia, Oligocene.

Diagnosis. First dorsal pterygiophore inserted in 4th or 5th interneural space (in the third in other *Sarda* and most other scombrids).

Referred material. PIN 1413-34, river Gumista, Abkhazia, Georgia, Middle Oligocene (Miatly-Mutsidakal Horizon); PIN 1413-45, **Holotype**, river Belaya, Caucasus, Russia, Late Oligocene: Chattian (Morozkina Ravine Horizon).

Description. Body slender. PIN 1413-34 possesses 25 precaudal vertebrae Total number of vertebrae could not be verified with specimens studied, but reported as 41-42, of which 22-23 precaudal, in Bannikov (1985). Interpelvic process shorter than pelvic fin. Pelvic fin small, with 1 spine and 5 soft rays. Pectoral fin with 15 rays, pointing slightly dorso-caudad. First dorsal interneural inserted in 4th or 5th interneural space. First dorsal fin with XVII (XV-XVI according to Bannikov) spines.

Genus *Stereodus* Owen, 1865

Stereodus Owen, 1865: 145.

Stereodon Cooke, 1891: 546-547.

Diagnosis. The affinities of *Stereodus* seem to be within Sardini. Possession of hypural plate with most elements (apart from hypural 5 (partially) and parhypural) fused together and the short vertebrae indicate that. Vertebrae short. PU2-4 abruptly shortened. Other vertebrae as most as long as deep. Differs from the (possibly) similarly sized *Gymnosarda* by having unfused parhypural at hypural plate, and from other (smaller) Sardini by having hypural plate which is less trianguar and more diamond-like, with all margins straight as opposed to distally swollen.

Type species. Only one species knnown, see below.

Species composition. Contains just one species, described below.

Remarks. Woodward (1901) mentioned that *Sterodus* reminds him of *Sphyraenodus conoideus* Von Meyer, 1846, as described by Von Meyer (1851) (p. 281, pl. 33, Fig. 13). However, a comparison with genus *Sphyraenodus* does not hold. Typical *Sphyraenodus* teeth are conical, straight, slightly oval and with basal striations. *Stereodus* teeth can be almost circular. *S. conoideus* is also not a *Sphyraenodus* (see descrption of *Sphyraenodus*).

Stereodus melitensis Owen, 1865 (Fig. 7.39)

Stereodus melitensis Owen, 1865: 145. Type loc. Malta, Miocene.

Stereodon melitensis Cooke, 1891: 546. Type loc. *ibid.*

Diagnosis. As for genus.

Referred material. BMNH P6207a, Malta, Early Miocene (Burdigalian-Landinian, vertebrate beds of *Globigerina* Limestone). Age of limestone verified with Steininger (1985).

Description. The studied specimen concerns a caudal region. Teeth which are associated with *S. melitensis* are described by Owen (1865). Vertebrae short, at most as long as deep. Lateral sides of centrums indented, but with elevated lateral ridge along middle of centrum, which is damaged on most present centrums. It is not clear if these ridges have formed a bony caudal keel. Present are caudal skeleton and centrums PU2-8. In all present vertebrae ventral and haemal spine flattened, broadened and partially overlie next vertebra. PU2-4 abruptly shortened. Caudal fin supported by neural and haemal spines of PU2-4, the one epural present, hypural complex and parhypural. Hypural plate fusion of urostyle, uroneural and hypurals 1-4. Hypural 5 fused to plate only at its basis. 40 mm long. Anterior dorsal process of uroneural damaged. Parhypural not fused to plate. Anterior head small, damaged. Hypural plate with diamond-like shape, anterior

margins longer than posterior ones, all margins straight. Plate bears marks of once present caudal fin rays: possessed hypurostegy. Plate damaged caudally, but does not seem to have caudal notch. Tail fin (semi) lunate.

Remarks. The size of the teeth of *S. melitensis* already indicated its large size. Also the hypural plate is rather large: 40 mm long. However, *Stereodus* may not have been unusually large for a Sardini. The largest Sardini known today is *Gymnosarda*, which can reach lengths up to 1500 mm (Collette & Nauen, 1983). A *Gymnosarda* of 860 mm has a hypural plate of 25.6 mm long (BMNH 1934.3.31). Exttapolationg thus, A maximum length *Gymnosarda* would have a hypural plate of 44.7 mm long.

Specimen BMNH P6207 has been catalogued as a *Stereodus melitensis*, but it now seems to concern an unidentified species of *Scomberomorus* (see *Scombermorus* sp., above).

A specimen of single tooth is stored as *Stereodon melitensis*: BMNH P10563, St. Paul's Bay, Malta, Early Miocene (Burdigalian-Landinian, vertebrate beds of *Globigerina* Limestone). This damaged tooth is certainly no *Stereodus*: It possesses one lateral cutting edge, a basal diameter of 8 mm and a crown of at least 17 mm which does not seem to be hollow. This is unlike a tooth of any known scombroid, let alone a fish. I have not carried out an SEM analysis, but where tooth is damaged basally, there seems to be one single layer of outer enamel. In fishes however, three distinct outer layers are readily distinguishable. The first identification of *Stereodus* known, by A.L. Adams (Owen, 1865) was of a crocodilian. BMNH P10563 resembles a crocodilian, but the apparent pattern of ridges on enamel (characteristic for crocodilians) is a deceiving image created by cracks in surface: the enamel is smooth. Furthermore, the tooth possesses one cutting edge instead of two. The tooth seems to be sauroid, but it is at this point impossible to say to which member of the Reptilia it belongs (Cuny, pers. comm., 1999).

Sardini indet.

Diagnosis. Supratemporal groove extending to anterior apex of frontal, orbit low (expressed here by shallow basisphenoid) and dorsally not much arched.

Referred material. BMNH P9459, Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. One neurocranium. Skull wide: 197 mm long and maximum preserved width 145 mm (real width not known through damage). Skull shallow: dorsal margin of orbit, skull roof and ventral outline of parasphenoid poorly arched. Basisphenoid broken, but would be short for sure: pedicel that connects

alisphenoid to parasphenoid would have been approximately 9 mm deep. In an *Auxis* cranium of only 52 mm long (of KAM 3), for example, this pedicel is 7 mm deep. Absence or presence of pineal window not clear from specimen, but would have been small if present. Pineal region around symphysis of frontals swollen. Lateral, upturned ridges of groove are damaged and thus missing in fossil, but there is no sharp anterior ridge that marks anterior margin of supratemporal groove. Postero-superior fossa clearly posterior of middle of orbit. Dorsal margin of orbit very poorly arched, almost straight. Frontoparietal window absent. Ethmoid damaged, but has tapered rostrad-pointing anterior margin. Pterotic and hindermost portion of skull damaged. Vomer damaged, but, but seems identical to one of typical tuna or bonito. Anterior head of vomer bifurcated into two, short and blunt protuberances that are anteriorly widely spaced. Vomerine tooth plate absent. Probably present in life but damaged in fossil. Vomerine tooth plate would not have protruded in life, as in Scomberomorinae. Parasphenoid straight lin lateral view. No prootic pit-covering outgrowths of sphenotic (as seen in Thunnini). Because of the relative flatness of skull roof, straightness of dorsal margin of orbit, and parasphenoid, one can say that orbit was relatively shallow.

Remarks. Resembles a Sardini at first sight, through the wideness of the skull, the lenght of the supratemporal grooves and the absence of frontoparietal fenestra. These features could also identify the specimen as a primitive tuna like *Auxis*. However, the flatness of the dorsal margin of the orbit and the shallowness of the orbit as a whole are apomorphies that define Sardini in relation to more primitive scombroids like the scombrinae. Tunas do not possess such an apomorphy, their orbits are much arched and deep. The specimen resembles most a *Gymnosarda*, which has a wide skull and is also large. A *G. unicolor* specimen, BMNH 1934.3.31, has a forklength of 860 mm. However, typical apomorphies of *Gymnosarda*, such as two tooth patches on the tongue and a fused parhypural are not found and the orbit in this specimen seems somewhat too flat.

This specimen was originally labelled as *Eocoelopoma colei*, but it has nowhere been documented. This is however no *Eocoelopoma*, because of the protruding ethmoid, the long supratemporal groove and the posterior postero-superior fossa. Also, the antrior part of the frontal is not remarkably thickened and there are no clear traces of a fine ornamentation. I suppose that the wideness of the skull and the overall appearance have led to a previous wrong diagnosis of *E. colei*.

Sardini? indet.

Referred material. BMNH P45150, Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. Moderately large skull, 135 mm long, maximum width 90 mm. Anterior head of vomer short with slightly emarginated anterior margin, pronounced lateral articular processes (for articulation with maxilla and premaxilla), moderately narrow and ovoid tooth plate on aterior head, bearing minute teeth.
Remarks. Previously identified as *Eocoelopoma colei*. Although this specimen is nowhere documented, the identification as *Ecoelopoma colei* as on the collection label is understandable. The antero-lateral margins of the frontals are rounded and decorated with fairly widey spaced curved lines. However, this frontal morphology could also well correspond with some Thunnini or Sardini. The actual apomorphy that would identifiy this specimen as an *Eocoelopoma*, the anteriorly placed postero-superior fossa, are buried in the matrix. Also, the size of the specimen is larger that the two specimens of *E. colei* that have been positively identified (see above: 80 mm long). Furthermore, the vomerine tooth plate of *Eocoelopoma* normally protrudes, as in *Eocoelopoma gigas* specimen BMNH 33305 and the specimens of *E. curvatum*: that I observed. Hence, the specimen is more likely to be a Sardini or Thunnini. Judged by the size of its teeth, the specimen is identified as a Sardini. Based on skull shape and vomer this specimen resembles most an *Orcynopsis*. However, this identification cannot be certified.

Tribe **Thunnini** Starks, 1910

Genus *Thunnus* South, 1845

Thynnus Cuvier, 1817: 313 (*non* Fabricius, 1775).

Orcynus l.c.: 314 (*non* Rafinesque-Schmaltz, 1815).

Thunnus South, 1845: 620.

Albacora Jordan, 1888: 180.

Germo l.c.: 180.

Parathunnus Kishinouye, 1923: 442

Neothunnus l.c.: 445.

Alciola Jordan, 1925: 27.

Kishinoella Jordan & Hubbs, 1925: 219.

Semathunnus Fowler, 1933: 163.

Diagnosis. Frontoparietal fenestrae and pineal window present, first vertebra fused to basioccipital. Forklength up to 2700 mm. Differs from other Thunnini by having shorter pterotic spines, denser scale covering and a less crescent-shaped preoperculum.
Type species. Thunnus thynnus.
Species composition. Seven Recent species are normally recognised. Collette (1999) suggests that *Thunnus thynnus orientalis* (Temminck & Schlegel, 1844) is

to be recognised as a species in its own right. This would make the amount of Recent *Thunnus* species eight. Seven fossil species are known from across Europe and the former USSR, from the Eocene to the Miocene.

***Thunnus* sp.** (Fig. 7.40)

Thynnus thynnus Woodward, 1901: 455 (BMNH P8737 *non* Cuvier, 1817).

Thynnus scaldisi Woodward, 1901: 455 (BMNH P5583, P9453).

Diagnosis. Large vertebrae: measured between 35 and 42 mm long.

Referred material. BMNH 41989 (labelled as *Thynnus thynnus*), Lea Vally, near Tottenham, England, Middle Pleistocene (Pebble Gravel); P5583, Suffolk, Piacenzian (Red Crag); P8737 (labelled as *Thynnus thynnus*), East Runton, Norfolk, England, Early Pleistocene (Lower Forest Bed Formation); P9453 (labelled as *Thynnus scaldisiensis*), Aldborough, Suffolk, England, Piacenzian (Coralline Crag).

Description. Isolated centra (BMNH P5583, P8737, P9453) and three associated vertebrae (BMNH 41989, Fig. 7.40). Centrum BMNH P5583 is a caudal (non-preural) vertebra, 35 mm long and 31 mm deep and 39 mm wide (including lateral keel). BMNH P9453 is a centrum which is 42 mm long. 36 mm deep and 45 mm wide including keel). BMNH P8737 has similar dimensions, but is 50 mm wide including lateral keel. BMNH P41989 consists of three articulatedd vertebrae, which *in vivo* had been amongst the most caudal in the vertebral column. These are not preural centra, because although they shorten progressively, the shortening is not abrupt. Centra deeply indented dorsal and ventral of lateral midline.

Remarks. Woodward (1901) described BMNH 41989 and P8737 as *Thunnus thynnus* (Linnaeus, 1758) and BMNH P9453 as †*Thynnus scaldisi* (correct name *T. scaldisensis*) (Storms, 1890). I am confident, based on their dimensions, morphology and size, that these specimens do belong to *Thunnnus*. Centra of Sardini are shorter and their lateral caudal keels less well developed. Other Thunnini genera are considerably smaller that *Thunnus*. Storms (1889), describes vertebrae that differ slightly from *Thunnus thynnus*. Initially, Storms seems to consider the differences with *T. thynnus* insufficient to create a new species, after which he contradicts himself by erecting a new species *Thynnus scaldisi* for the specimens, because of their Tertiary age. Judging the size of Storms' specimens, complete individuals might have been as large as *T. thynnus* (maximum length 3 m, Collette & Nauen, 1983). There are no synapomorphies that distinguish *T. scaldisensis* from any other *Thunnus*. I believe that without other material, *T. scaldisensis* is an invalid name. The specimens which Woodward (1901) described as *T. scaldisi* do not reveal anything which Storm's specimens already had.

According to Woodward, *T. scaldisensis* is somewhat smaller than *T. thynnus*, but the specimens he used to describe these species contradict that (see also dimensions in description above).

Gen et sp. **indet.,** ***non Thunnus*** (Fig. 7.41)

Diagnosis. Large corselet scales on opercular bones. Preoperculum strongly bent into crescent, operculum roughly diamond-shaped.
Referred material. USNM 17881 (Fig. 7.41), 3.3 miles N of Hannah Lake, Yakataga District, Alaska, U.S.A., Oligocene.
Description. Rather well preserved two-dimensional fossils of skull in slab. Teeth not preserved. Thunnini possess small teeth that damage easily. Eye sclerotics well preserved, encompassing circular space where eye has been. Large elongated cheek scales immediately posterior of orbit. Preoperculum wide, but suddenly tapered at both anterodorsal and anteroventral apex, strongly bent into crescent-shaped structure. Operculum roughly diamond-shaped, ventral margin somewhat lengthened and tapered. Traces of flakes on opercular bones, which, especially on subopercula appear to be remnants of corselet scales.
Remarks. The specimen in question is labelled as *Euthynnus* sp. Based on shape of opercular bones and traces of large scales on them, I conclude that this concerns a specimen of Thunnini. This is not a *Thunnus*, whose preoperculum is not thus strongly bent, but more shaped as a slightly curved banana. There are however no distinguishing apomorphies that determine whether this concerns an *Allothunnus*, *Euthynnus* or *Katsuwonus*. Adding to the above statement that this is not a Thunnini, I can confirm that it is not an *Auxis* either. *Auxis* skulls are only a few centimeters long.

Gen. et sp. **indet. 2**

cf. Eothynnus salmoneus Woodward, 1901: 458.

Diagnosis. Preural vertebra 4 more than 1.5 times longer than preural vertebra 3.
Referred material. BMNH P4300, Sheppey, England, Early Eocene: Ypresian (London Clay).
Description. Fourth and third preural vertebrae. One long centrum (fourth), and one radically shortened (third). Fourth preural centrum 45 mm long, third preural centrum 12 mm.Vertebrae do not present many details. Cross-section of third preural: horizontal axis slightly longer than vertical axis. This cannot be measured in fourth preural. Bony median caudal keel preserved.

Remarks. Woodward (1901) described this specimen as being probably *Eothynnus*, without mentioning on which apomorphies this is based. This specimen concerns definitely a tuna, but without information on other body parts than these vertebrae, no further identification can be made.

Genus et species **indet. 3** (Fig. 7.42)

Thunninae gen. indet., Bannikov, 1985: 66, pl. VIII, fig. 5.

Diagnosis. Preural vertebrae 2-4 abruptly shortened.

Referred material. PIN 3363-96 (Fig. 7.42) , river Belaya in Abadzekhskaya village, Caucasus, Russia, Early Oligocene: Rupelian, (Pshekha Horizon).

Description. See Bannikov (1985).

Remarks. The exact identity of this enigmatic fossil cannot be certified. Only in Thunnini are the preural vertebrae so abruptly shortened. The structure of the hypural plate seems mysterious. Bannikov (1985) assumed that this was the shape of a mature, unndamaged hypural plate and described it thus. I am however uncertain about these notions. The parhypural, if it is preserved undamaged, is remarkably small. The outline of the hypural plate is partially obscured by the matrix, makinng it uncertain whether the outline is fully preserved or damaged. I do not know the morphology of juvenile Thunnini caudal complexes but the fossil in question might be one, also taking its size into account.

Subfamily **Acanthocybiinae** Starks, 1910

This tribe includes *Acanthocybium* and its fossil relatives. The fossils in question are thought to be related to *Acanthocybium* based on their dental and vertebral morphology (see descriptions below).

cf. Acanthocybium (Fig. 7.43)

Scomberomorus saevus, Bannikov, 1982: 143; 1985: 37, fig. 17 Γ and ∂ (*pro parte*, PIN 1878-2). Type loc. Ustyurt, Kazakhstan, Eocene.

Referred material. BMNH P27010, Sheppey, England, Early Eocene: Ypresian (London Clay) (Fig. 7.43a); PIN 1878-2 (Fig. 7.43b), Western extremities of Ustyurt Plateau, Kazakhstan (Shorym Svita), Late Eocene: Priabonian (**paratype** of *Scomberomorus saevus*). USNM 498669, South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A. (Fish Stratigraphic

Column, Pungo River Formation), Miocene: Late Burdigalian to Early Serravalian; USNM 2667, 498663, 498667, 498668, 498672 and 498673, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A. (Yorktown Formation), Early Pliocene: Zanclean.

Description. Hypural plate, made up of the fusion of urostyle, hypurals 1-4 and parhypural. As in *Acanthocybium* and Scomberomorinae, this species might have had a rudimentary fifth hypural associated with the hypural plate but not fused to it. This element is missing in all these fossil specimens. Plate diamond-shaped, sides almost equal in length. Height (66-76 mm, measured on 4 specimens), on average 2.1 times length (measured on 3 specimens). Caudal outline of diamond not swollen outwardly; all sides more or less straight. Posteriorly a clearly discernible notch. Markings made by the fin rays crossing the plate visible as shallow grooves, running parallel to rostral sides of diamond. Parhypurapophysis making angle of about 45° with horizontal axis, but its posterior process running parallel to horizontal axis. Uroneural not fused with urostyle. Cross-section of urostyle clearly ovoid with the long axis horizontal (as in *Scomberomorus* and *Acanthocybium*).

Remarks. The first hypural plate to be characterized by this description was PIN 1878-2. At a later stage, I studied the above mentioned specimens in the USNM and BMNH. Because of their similarity, they might belong to the same species, although, judging the different locations of the fossils, that is not very likely. The fossils show a striking resemblance to *Acanthocybium solandri*, the only species of a monospecific genus. Hypural plates of Scombermorinae and *Acanthocybium* consist of the fused hypurals1-4, and usrostyle and possess a caudal notch. Hypural 5 and the uroneural are not fused to the plate and are autogenous in the caudal skeleton. In *Acanthocybium* the parhypural is fused to the plate. The specimens in question can however not be assigned to *A. solandri*. Compared with *A. solandri*, these fossil plates are slightly shorter, have longer urostyles, slightly bigger caudal notches and the dorsal half never protrudes beyond the ventral half. Height of hypural plate between 66 and 76 mm, while in *A. solandri* hypural plate heights are between 34.5 and 41.0 mm (pers.obs.). Compared to more primitive scombrids, *A. solandri* possesses the apomorphous characters of fused elements into a hypural plate and a fused parhypural. Although the new species possesses these characteristics, it is clear, based on its dimensions that it is not an *A. solandri*. It cannot even be argued that it is an *Acanthocybium*. *Gasterochisma* has a hypural plate consisting of hypurals 1-4 completely and hypural 5 partially fused, the uroneural, urostyle and parhypural. Compared to *Acanthocybium*, *Gasterochisma* has a more advanced hypural plate, because the uroneural is also fused to into the complex. All that can be argued, hence, is that the fossil hypural plates discussed here are plesiomorphous compared to those in *Gasterochisma*, as is that of

Acanthocybium. Moreover, other (fossil) representatives of the Acanthocybiinae such as *Scomberodon* and a new genus (see below) have the uroneural fused to the plate. The fossils discussed here cannot be assigned to *Acanthocybium* based on the symplesiomorphy of an unfused uroneral.

Genus ***Gigantothazard*** gen. nov.

Etymology "Thazard" is a French vernacular name of *Acanthocybium*. This new genus resembles *Acanthocybium* in its dentition, but is much larger.

Diagnosis. Teeth laterally flattened, tightly packed and blunt-tipped, anteroventral emargination in dentary. Differs from *Acanthocybium* in much larger size, teeth with smooth cutting edges, and the absence of an anteromedian dentary notch.

Type species. Only one species is known (see below).

Species composition. Only one species known, described below.

Remarks. Most scombroids have more or less widely spaced, sharp conical teeth. *Gigantothazard*, *Acanthocybium*, *Scomberodon* and a new genus described below have tightly packed blunt teeth with slightly rounded apices. This is further derived in *Acanthocybium*, whose teeth are serrated. This would mean that *Gigantothazard* would be represented by only one character in the matrix. Its apomorphous sistergroup, *Acanthocybium* is well represented in the matrix, so there seems to be an imbalance there. Hence, I decided to leave *Gigantothazard* out of the analysis until more data are available. However, I believe I can assess *Gigantothazard* as an acanthocybiin, based on dental characters.

Gigantothazard aurorensis gen. et sp. nov. (Fig. 7.44)

Etymology. Species named after only location known so far, Aurora, North Carolina, U.S.A.

Diagnosis. As for genus.

Holotype. USNM 319668, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., dentary, Early Pliocene: Zanclean (Yorktown Formation) (Fig. 7.44a).

Referred material. Apart from holotype: USNM 498666, 498665, 498670, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Early Pliocene: Zanclean (Yorktown Formation).

Description. Material consists of jaw fragments, completest of which is the holotype. Resembles *Acanthocybium*, but is much larger (Figs. 7.44a, b). In fossil, distance between anterior margin first tooth and posterior margin 20th tooth is

135.5 mm. In *Acanthocybium* specimens (USNM 270403, 270394 and 270398) of 1202-1420 mm forklength, distance is between anterior margin of first and posterior margin of 10th tooth (could not be measured up to 20th tooth because of articulation with upper jaw) 34.5-39 mm. If *Gigantothazard* was an *Acanthocybium*, extrapolating these figures lead to the estimate that *Gigantothazard* reached a forklength of 4.5 m. The largest *Acanthocybium* specimen I have studied has a forklength of 1.42 mm (USNM 270398). The longest reported *Acanthocybium* is 2.1 m long (Collette & Nauen, 1983). Teeth in dentary tightly packed, semiconical, laterally flattened short and blunt-tipped, cutting edges smooth. Dentary with anteroventral emargination.

cf. Gigantothazard (Fig. 7.45)

Diagnosis. Hypurals 1-4 , urostyle and parhypural fused, urostyle wider than deep, depth of hypural plate approximately 90 mm.
Referred material. USNM 498675, no data.
Description. Damaged hypural plate (Fig. 7.45). Maximum preserved depth 88.6 mm, maximum preserved length (including urostyle, excluding parhypurapophysis) 53.2 mm. Hypurals 1-4, parhypural and urostyle fused. Damage on dorsal tip of plate probably result of broken off hypural 5, which would have been partially fused to plate. No trace of uroneural but also no anterodorsal projection on urostyle, so uroneural presumed missing and autogenous. Cross section of urostyle wider than deep. Anterior margins of plate fairly straight, posteror margins with mid-posterior swelling. This region of plate damaged, at where persumed caudal notch would have been. Grooves in surface of hypural plate is evidence for hypurostegy.
Remarks. An exact identification of this specimen is not possible. In its characteristics it is similar to a hypural plate of and *Acanthocybium*, but is much larger. *Acanthocybium* of between 1068 and 1242 mm (USNM 270394, 270397, 270399) have hypural plates that are between 34.5 and 45 mm deep. Judging by its size and characteristics, it is possible that this fossil belongs to *G. aurorensis*. However, the age and location of the fossil are unknown, and one can only guess whether it was found in association with *Gigantothazard* remains.

Genus ***Palaeocybium*** gen. nov.

Cybium Storms, 1895: 160 (*non* Cuvier, 1829).

Diagnosis. Teeth blunt-tipped and tightly packed, in a double tooth row. According to Storms (1895) vertebrae had large midlateral dent.
Etymology. *Cybium* is a synonym of *Scomberomorus*, which according to some in closely related to *Acantocybium*. Kishinouye (1923) included both *Scomberomorus* and *Acanthocybium* in the family "Cybiidae". *Palaeo* is Latin for "old".
Type species. Only one species known, described below.
Species composition. The type species only.

Palaeocybium proosti comb. nov. (Fig. 7.46)

Cybium proosti Storms, 1895: 160. Typ. loc. nr. Brussels, Belgium, Eocene.

Cybium cf. proosti Casier, 1966: 298: pl. 47, fig. 2.

Diagnosis. As for genus.
Referred specimens. BMNH 36166, Sheppey, England, Early Eocene: Ypresian (London Clay).
Description. Very fragmentary and incomplete fossil, but possessing peculiar apomorphy. Only jaw bones preserved. Maxilla and premaxilla tightly interlocked, forming non-protractile complex. Teeth in double rows. Outer tooth row consists of minute laterally flattened, blunt-tipped semiconical teeth. Interspace between outer row teeth approximately width of one tooth. Inner row teeth much larger, similar in shape to outer teeth, tightly packed.
Remarks. The description of this specimen perfectly matches Storm's (1895) description of *Cybium proosti*. Casier (1966) identified the specimen as *Cybium cf. proosti* without mentioning the reasons for uncertainty regarding the specific identification. Before Casier's description, *Cybium proosti* was only known from the Lutetian of Belgium. *P. proosti* shows a peculiar apomorphy in that it has a double tooth row, which is unique for the Acanthocybiinae.

Gen. et sp. **indet.**

Neocybium sp. Bannikov, 1985: 40, pl. 4, fig. 3 (PIN 1878-5).

Diagnosis and description. Hypural plates that show the character combination of *Scomberodon* and *Neocybium* (hypurals 1-4, uroneural and urostyle fused, urostyle wider than deep, parhypural autogenous). Teeth laterally depressed.

Referred material. BMNH 241686c and 38883, Sheppey, England, Early Eocene: Ypresian (London Clay); one of P14029, Barton, Hampshire, England, Bartonian (Barton Clay). USNM 286186, 498664, 498672, 498677, Lee Creek Mine, South side of Pamlico River, Aurora, Beaufort Co., North Carolina, U.S.A., Early Pliocene: Zanclean (Chesapeake Group, Yorktown Formation). PIN 1878-5, Mangyshlak peninsula, Kazakhstan, Late Eocene: Priabonian (Shorym Svita).

Remarks. Scomberodon (Van Beneden, 1871) has been synonymised with *Scomberomorus* (see Leriche, 1910). However, the presence of a midlateral dent in the vertebrae and the fact that its uroneural is fused to the hypural plate clearly distinguish *Scomerodon* from *Scomberomorus. Noecybium* Leriche, 1908 is known from remains of the skull and the axial skeleton that resemble those of *Scomberodon*. Apparently, there is nothing that separates hypural plates of *Scomberodon* and *Neocybium*. The difference between the two lies in their vertebral column. *Neocybium* has a large, fully developed midlateral depression in its vertebrae. In *Scomberodon*, this depression is small and partially developed (Leriche, 1910). The dentition of *Neocybium* and *Scomberodon* resembles that of *Scomberomorus* in being somewhat depressed laterally. *Neocybium* and *Scomberodon* differ from *Scomberomorus* in that their teeth are somewhat smaller and more tightly packed, although not as tightly as in *Acanthocybium* and less blunt-tipped. I cannot see any significant differences between the dentition of *Scomberodon* and *Neocybium*, as figured by Leriche (1910), hence the premaxilla PIN 1878-5 cannot be assigned to genus *Neocybium*, as was done by Bannikov (1985).

Subfamily EOTHYNNIDAE subfam. nov.

This fossil subfamily which contains only one genus, *Eothynnus*, is characterised by multiple rows of small teeth and long supratemporal grooves. Because of this combination of characters, *Eothynnus* does not fit in any known scombroid subfamily.

Genus *Eothynnus* Woodward, 1901

Coelocephalus Agassiz, 1833-44: 139; Agassiz, 1845 (*nomina nuda*, *non* Gilbert & Cramer 1897).

Eothynuus Woodward, 1901: 457.

Diagnosis. Supratemporal groove extending to anterior tip of frontal. Multiple tooth rows. Opercular bones covered by large scales. Resembles, in dorsal view, a Sardini or Thunnini, by its long supratemporal groove and long cranial crest. Contrary to Thunnini and Sardini, *Eothynnus* does not have cepahlic foramina.

Because of the lack of these foramina, the dorsal side of an *Eothyunnus* skull also resembles *Scomberomorus*. None of these Recent taxa, however, have multiple tooth rows.

Type species. Only one species known (see below).

Species composition.Only one species known, described below.

Eothynnus salmoneus Woodward, 1901 (Fig. 7.47)

Coelocephalus salmoneus Agassiz, 1833-44: 139; 1845: 308 (*nomina nuda*).

Eothynnus salmoneus Woodward, 1901: 457. Type loc. Sheppey, England, Eocene.

Diagnosis. As for genus.

Referred material. BMNH 28757 (Fig. 7.47) and P26899, Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. Lachrymal stout but short: shorter than diameter of orbit (Fig. 7.47a). Supratemporal groove extending long rostrad, until anterior tip of frontal (Fig. 7.47b). Cephalic foramina absent. Pterotic a short wing. Maxilla-premaxilla complex non-protractile. Upper and lower jaw with teeth, in minute, circular sockets and multiple rows ("cluster of minute teeth", Woodward, 1901), no fangs. Last branchiostegal ray not unusually flattened or widened. Unclear if operculum has postero-dorsal indentation, but opercular bones seem, other than this uncertainty, identical to the ones of *Scomber*: short but deep and operculum strongly extending ventrad and strongly tapering. Only few vertebrae preserved, resembling those of *Acanthocybium*: short (about twice as high as long), two median ridges along sides of centrum, seperated by deep groove. Middle of centrum almost as deep as maximum diameter. Specimen BMNH 28757 with large scales preserved on operculum (Fig. 7.47). Whether as part of a complete covering of massive scales or as part of anterior corselet is unclear.

Remarks. Without mentioning any reason, some fossil specimens of vertebrae are assigned to this species by Woodward (1901). Neither of the two specimens discussed here (BMNH P4300 and P4301) can be identified as *Eothynnus*. BMNH P4300 is further down described as Thunnini indet. BMNH P4301 concerns one single centrum which might have belonged to either an *Acanthocybium* or an *Eothynnus*. I am not able to distinguish between the two on the basis of one centrum.

Subfamily XIPHIINAE Swainson, 1839
Tribe **Xiphiorhynchini** Regan, 1909

A fossil billfish family, known of rostra, skull parts and vertebrae. The most striking feature is the presence of four nutrient canals in the rostrum, while in istiophorins there are two and in *Xiphias*. Schultz (1987) erected a new xiphiorhynchin genus *Thalattorhynchus*, based on a fossil rostrum. The assignment of this "new" genus is primarily based on the eccentrically-placed nutrient canal, an anomaly previously found in Istiophorins. I have seen rostra of Recent *Tetrapturus*, in which the cross-section close to the apex shows just one of the normally two lateral nutrient canals. I suspect that "*Thalattorhynchus*" is an unidentifable istiophorin. Hence, the Xiphiorhynchini are a monogeneric tribe, containing *Xiphiorhynchus*.

Genus ***Xiphiorhynchus*** Van Beneden, 1871

Tetrapturus Agassiz, 1835a: 303 (*non* Rafinesque-Schmaltz, 1810).

Tetrapterus Agassiz, 1833-44: 91, pl. 31 (*non Tetrapturus* Rafinesque-Schmaltz, 1810).

Histiophorus Cope, 1869: 310 (*non* Cuvier, 1832).

Xiphiorhynchus Van Beneden, 1871: 499.

Xiphiorrhynchus Winkler, 1874: 304 (*err. typ.*).

Diagnosis. Rostra ovoid in cross-section, with four nutrient canals (Figs. 7.48, 7.49). Central canal extends far anteriorly.

Type species. *Xiphiorhynchus elegans* Van Beneden, 1871.

Species composition. Schultz (1987) mentions a total of seven species, occurring from the Late Palaeocene to the Middle Eocene. *Xiphiorhynchus parvus* Casier, 1966 is here described as an unidentifiable istiophorin. *Xyphiorhynchus priscus* (Agassiz, 1844) and *X. eocaenicus* are described below, and a specimen labelled as *X. ?antiquus* is mentioned.

Remarks. The identity of the various fossils that have been called *Xiphiorhynchus* is problematic, because there are no articulated parts known. Many specimens in the collection of BMNH which are labelled are not *Xiphiorhynchus*: I have identified these remains as *cf. Gymnosarda* sp., Istiophorinae indet., *Scomberodon*, *Scomberomorus*, and one specimen could not be identified at all. Woodward (1901) mentioned a few vertebral remains which he thought could be vertebrae of *Xiphiorhynchus*, probably because they are "Xiphioid vertebral centra" found in sediments of the same age and the same place as *Xiphiorhynchus priscus*. Of the specimens mentioned by Woodward I have seen BMNH 30530 and also centrum BMNH 32570 (Fig. 7.50), which is labelled *Xiphiorhynchus cf. priscus*. They resemble vertebrae of *Xiphias*, in that they are stout, elongated and circular in cross-

section. However, because these vertebrae are not known to be found associated with remains that are surely *X. priscus*, it is better to consider these vertebrae unidentified. None of the hypural plates labelled as *Xiphiorhynchus* in the collection of BMNH could be assigned (with certainty) to that genus and are described elsewhere as other taxa or as unidentified taxa.

The name *Xiphiorhynchus* was first given to remains of billfish rostra with four nutrient canals (Figs. 7.48a, 7.49a). Agassiz (1833-44) was the first to associate the rostra with certain skull remains. It must be mentioned, though, that he supposed these remains concerned those of *Tetrapturus*. Rostra and skulls are thus associated on the basis of resemblance to *Tetrapturus*. However, it is proven that the fossils in question do not concern *Tetrapturus*, and it might be that the various bills, skulls and vertebrae have nothing to do with each other. It has been in doubt for some time whether they do indeed belong together (see Fierstine, 1974). However, I do believe that a substantial portion of the remains can indeed be assigned to *Xiphiorhynchus*. Two skulls, BMNH P26990 (Fig. 7.49b) and BMNH P13056 (Fig. 7.49c) have teeth preserved on their premaxillae.These teeth are small, almost villiform cones in multiple rows. Skull BMNH 28711 (Fig. 7.49d) has the posterior end of its rostrum preserved. In there, one can see a pair of nasals (premaxillae *sensu* Casier, 1966) which are not fused along the midline of the bill. In *Xiphiorhynchus* bills there is a pair of large unfused bones on the dorsal surface (Fig. 7.49a), which I interpret as the nasals. It looks to me as if these bills would fit perfectly on a skull such as the one pictured in Fig. 7.49c. I believe there is enough evidence to support that the rostra and craniums in question are indeed associated.

The rostrum shows a mix of characters, known from either istiophorins or *Xiphias*. The rostra are ovoid in cross section, often a little more circular than in istiophorins. *Xiphias* bills are dorsoventrally flattened. The pattern of bones (compare Figs. 7.48a, 7.49a) however, seems to match more that of *Xiphias* than that of istiophorins. Just as in *Xiphias*, the nasals are situated directly anterior of the ethmoid, while in istiophorins the ethmoid is laterally flanked by the nasals (see Fig. 5.26).

Xiphiorhynchus eocaenicus (Woodward, 1901) comb. nov. (Fig. 7.48)

Histiophorus eocaenicus Woodward, 1901: 495, fig. 18. Type loc. Bracklesham, England, Eocene.

Diagnosis. Four nutrient canals small and difficult to distinguish. In *X. priscus* the canals are clearly visible. While the rostrum of *X. priscus* is almost circular, that of *X. eocaenicus* is more dorsoventrally flattened, almost as in istiophorins.

Referred specimens. BMNH P25744 (**holotype** of *Histiophorus eocaenicus*, Fig. 7.48), Bracklesham, England, Early-Middle Eocene: Ypresian-Lutetian (Bracklesham Beds).

Description. A description is given by Woodward (1901).

Remarks. Woodward (1901) referred to certain specimens of fossil rostra as *Histiophorus*, "for convenience of reference", meaning that their identity as *Istiophorus* was uncertain to start with. Among these specimens was the only specimen known of *X. eocaenicus*. Maybe Woodward thought that this could not be a *Xiphiorhynchus* because this bill is more flattened than that of *X. priscus*. However, the four nutrient canals are definitely an apomorphy of *Xiphiorhynchus*.

Xiphiorhynchus priscus (Agassiz, 1844) (Fig. 7.49)

Tetrapturus Agassiz (1835a): 303 (*non* Rafinesque-Schmaltz, 1810).

Tetrapterus priscus Agassiz, 1833-44: 91, pl. 31. Type loc. London Basin, Eocene.

Histiophorus priscus Cope, 1869: 310. Type loc. *ibid.*

Diagnosis. Four nutrient canals clearly visible, cross-section of rostrum always more than half as deep as wide.

Referred specimens. BMNH 3888, 28711 (Fig. 7.49d), 32387, P4300, P13506 (Fig. 7.49c), P26990 (Fig. 7.49b) and 36133a (Fig. 7.49a), Sheppey, England Early Eocene: Ypresian (London Clay); P12204, East shore, Selsey, England, Bartonian (Selsey Sands, Bracklesham Beds); P19492, Beltinge, Herne Bay, Kent, England, Early Eocene: Ypresian (London Clay).

Description. Detailed descriptions of various specimens are given in Woodward (1901).

Remarks. According to Woodward (1901) *Ommatolampes eichwaldi* Fischer de Waldheim, 1851 is questionably a synonym of *X. priscus*. I have seen neither the specimen nor the papers in which it is described.

***Xiphiorhynchus* sp.** (Fig. 7.51)

Diagnosis. Rostrum ovoid in cross-section, bone structure spongy, four nutrient canals.

Referred material. USNM 353509 (labelled *Xiphiorhynchus ?antiquus*), 6.4 km by road W. of Post Office at a few hundreds of meters N. of State Route 41, immediately W. of Tuckahoe Church, Jones Co., North Carolina, U.S.A., Early-Middle Eocene (Claibornain Castle Hayne Formation).

Description. Concerns a specimen of a billfish rostrum (Fig. 7.51) in the USNM collection. The specimen strongly resembles *X. priscus*, in that the cross-section is ovoid, but not strongly compressed dorsoventrally and therefore more circular than in istiophorins. The four small nutrient canals are clear to the naked eye, as in *X. priscus*. The bone structure is spongy, to a much higher degree than in other *Xiphiorhynchus* specimens I have seen. I cannot tell whether that is a consequence of the taphonomy of the specimen or a genuine feature. The specimen is labelled *X. ?antiquus*. I do not know why the specimen, nowhere referred to to my knowledge, is identified as probably *X. antiquus*. There may be apomorphies that I am not aware of. I have not managed to obtain any reference in which that species is described, and because of its resemblance to *X. priscus* I remain uncertain of its specific identity.

Tribe **Xiphiini** Swainson, 1839

Genus ***Blochius*** Volta, 1796

Blochius Volta, 1796: 53.

Diagnosis. Pelvic fins absent, lower and upper jaw both extremely elongated into a rostrum, both as long. Differs from other billfishes by amongst others large diamond-shaped scales. Other billfishes naked or almost (but: see *Pseudotetrapturus*, below).

Type species. *Blochius longirostris* Volta, 1796.

Species composition. Schultz (1987) mentions three species, all known from the Eocene. *B. longirostris* is by far the best known species and is described below.

Remarks. A review of *Blochius longirostris* is currently carried out by H.L. Fierstine and me, with Fierstine contributing mostly to the study of specimens. My contribution will predominantly be to the phylogenetic analysis. It is possible that this will present *Blochius* in a different light than it will be here, and conclusions about its phylogenetic relationships could be changed.

Blochius is normally included in the family Blochiidae. Traditionally, the blochiids are understood to consist of the genera *Blochius*, *Cylindracathus* and *Congorhynchus* Dartevelle & Casier, 1949 (see Schultz, 1987). Blochiids have been thought to be related to Recent billfishes (Schultz, 1987), although this is sometimes doubted (Patterson, 1993). *Blochius* is the only one of these genera of which complete skeletons are known; *Cylindracatnus* and *Congorhynchus* are only known of remains of their rostra. However, having studied these "rostra", I doubt very much whether they have anything to do with billfishes, or even with fishes. Reasons for this are given together with short descriptions, in the section "Family *incertae sedis*". It can be argued that *Blochius* resembles a needlefish, especially

because of its extremely elongated beak, in which both upper and lower jaw are just as long. In Recent billfish, the upper jaw is always longer than the lower jaw. Woodward (1901) considered family Blochiidae a part of the Blenniiformes. I believe, however, that there are enough synapomorphies to consider *Blochius* a billfish (see below). The cladistic analysis (Chapter 8) proved that the synapomorphies with *Xiphias*, such as the lack of pelvic fins, weigh heavily, hence *Blochius* and *Xiphias* are considered closely related and are both included in family Xiphiidae.

Blochius longirostris Volta, 1796 (Fig. 7.52).

Blochius longirostris Volta, 1796: 53. Type loc. Monte Bolca, Italy, Eocene.

Diagnosis. As for genus.

Referred specimens. BMNH 19940 (Fig. 7.52b, c) & P4142 (two counterparts) and P4141 (Fig. 7.52a), USNM 2695329, Monte Bolca, near Verona, Italy, Lutetian (Monte Bolca Formation).

Description. A description is given by Woodward (1901). Any differences observed are noted here. The specimens of *Blochius* that I have seen have no teeth preserved. However, Schultz (1987) mentioned two juvenile specimens in the Natural History Museum in Vienna which have numerous denticles. A photograph of specimen S40 of the Museo Civico di Storia Naturale, sent to me by H.L. Fierstine, seems to show small teeth as well. However, it is not certain that this specimen is indeed a *Blochius* (Fierstine, pers. comm., 1999). For the cladistic analysis, the The upper jaw-part of rostrum somewhat flattened, although not as extremely as in *Xiphias*. Fierstine (pers. comm., 2000) thinks that the rostrum is has parallel lengthwise grooves in its dorsal surface, which agrees with Schultz' (1987, fig. 3, also Fig. 5.23c). The bill of *Blochius* is somewhat flattened, although not as strongly as in *Xiphias*. I believe that Schultz' (1987) cross section of a *Blochius* bill which is not strongly enough flattened. Lachrymal large, longer than orbit diameter. Supratemporal groove short. Postero-superior fossa posterior of middle of orbit. Cranial crest absent. Pterotic short. No posterior projection on intercalar. Ceratohyal without ventral projections or ceratohyal window. Vertebrae not extremely constricted and neural and haemal spines not modified, as in istiophorins. First anal pterygiophore articulating with first haemal spine. Median caudal fin lepidotrichia enlarged and widely spaced, as in scombrids and Recent billfishes. Caudal fin, as in Recent billfishes and scombrids, hypurostegic. Epurals two in number, as in *Xiphias*. Procurrent spur, as in all scombroids, missing. Posttemporal with two anterior processes. Predorsal bones absent, as in all scombroids. First dorsal pterygiophore inserted in first interneural space, as in

istiophorins (I do not know the insertion point for *Xiphias*). There is one continuous dorsal fin, in which there seems no differentiation between a hard and a soft part. All dorsal fin elements, 46 in number (50 in Woodward), appear to be rigid and are thus interpreted as spines. Maximum depth of dorsal fin deeper than depth of head, as in some istiophorins. The covering of scales (Woodward's "dermal scutes") is heterogenous. Near the dorsal and near the ventral side of the fish there seem to be lateral line scales (see Fig. 7.52c), which resemble the stout, large scales on the lateral line of *Trachurus*. Scales around these apparent lateral lines large and scales around mid-lateral part of trunk smaller.

Tribe **Istiophorini** Lütken, 1875

Genus *Makaira* Lacépède, 1802

Makaira Lacépède, 1802: 688, pl. 13, fig. 3.

Machaera Cuvier, 1832: 43, pl. 3.

Macaira Nardo, 1833: 418.

Istiompax Whitley, 1931: 321.

Marlina Hisaki & Nakamura, 1947: 15 (*non* Grey, 1928).

Eumakaira l.c.: 16, pl. 2, fig. 2.

Orthocraeros Smith, 1956: 31, pl. 1, fig. 1.

Diagnosis. Nape (anterodorsal profile of head) elevated, makes angle of >45° with axis of individual, lateral apophyses of vertebrae developed into anterolateral transverse plate-like flanges, centrum strongly widened anteriorly.

Type species. *Makaira nigricans* Lacépède, 1802.

Species composition. Three Recent species are known: *M. mazara*, *M. nigricans* and *Makaira indica* Cuvier, 1832. No *Makaira* fossils are specifically known.

Makaira sp.

Diagnosis. Centrum strongly widened anteriorly.

Referred specimens. BMNH 30798, Sheppey, England, Early Eocene: Ypresian (London Clay) (Fig. 7.53); P21086-8, Alum Bay, Isle of Wight, Bartonian (Lower Barton Clay).

Description. Amphicoelous, elongated, narrow centrums, strongly constriceted medially: haemal arch excluded, centrum is, at narrowest point less deep than 30 % of maximum depth. Centrum at its deepest anteriorly, where suddenly deepened and being considerably deeper than posterior end. Transeverse section of anterior and posterior end of centrum almost circular in outline. Rib socket preserved.

Remarks. The centrums described above must have been amongst some of the first precaudal vertebrae in the vertebral column. More posterior vertebrae of *Makaira* have laterally expanded lateral apophyses. The rib socket confirms that these are anterior vertebrae.

Genus *Tetrapturus* Rafinesque, 1810

Tetrapturus Rafinesque-Schmaltz, 1810: 54, pl. 1, fig. 1.

Skeponopodus Nardo, 1833: 416.

Tetrapturutus Bonaparte, 1841: 19 (*err. typ.*).

Tetrapterus Agassiz, 1844: 7.

Tetraplurus Vérany, 1847: 492 (*err. typ.*).

Scheponopodus Canestrini, 1872: 112.

Histiophorus Philippi, 1887: 35, pl. 8, figs. 2-3 (*non* Cuvier, 1832).

Makaira Jordan & Evermann, 1926: 55. pl. 16.

Tetraperus Radcliffe, 1926: 112 (*err. typ.*).

Marlina Grey, 1928: 47.

Kajikia Hirasaka & Nakamura, 1947, 1947: 13, pl. 2, fig. 1.

Pseudohistiophorus De Buen, 1950: 171.

Lamontella Smith, 1956: 26.

Diagnosis. Bill with variety of lengths, sometimes barely lonnger than upper jaw, sometimes clearly longer, dorsal fin deeper than depth of head. Differs from *Istiophorus* which has much larger, sail-like dorsal fin. Some of the species of *Tetrapturus* have the shortest rostra amongts the billfishes.

Type species. *Tetrapturus belone* Rafinesque-Schmaltz, 1810

Species composition. Six Recent species are known, of which the validity of *Tetrapturus georgei* Lowe, 1840 is questioned (Nakamura, 1985). The enigmatic "Hatchet Marlin" is known from sightings only; there are no known specimens in ichthyological collections and the species is not formerly described, but Nakamura (1985) suspects it might be an aberrant form of *Tetrapturus albidus* Poey, 1860. Five fossil *Istiophorus* were previously known, from the Oligocene and Miocene, described as either *Tetrapturus* or *Pseudohistiophorus* by Schultz (1987). Two fossil *Tetrapturus* are described by Agassiz (1833-44) from the London Clay of Sheppey. Unfortunately I have not seen the specimens on which Agassiz based his descriptions. *Histiophorus rotundus* is below redescribed as a *Tetrapturus*.

Tetrapturus rotundus (Fig. 7.54)

Histiophorus rotundus Woodward, 1901: 495, fig. 18, no. 3.

Diagnosis. Bill short, acutely tapered and rather rounded in transverse cross-section.

Referred specimen. BMNH P8799 (Fig. 7.54), Cooper River, Charleston, South Carolina, U.S.A., Tertiary (Tertiary Phosphate Beds, more precise age indication unknown to me).

Description. Badly preserved, probably incomplete rostrum. The anterior 314 mm preserved. Surface rugose, with numerous lengthwise grooves. Borders of different bones badly worn. Transverse cross-section almost circular. Details of nutrient canals not preserved.

Remarks. This rostrum is diagnosed as *Tetrapturus* because of its abrupt anterior tapering. *Tetrapturus angustirostris* Tanaka, 1915 and *Tetrapturus belone* Rafinesque, 1810 have short bills, which are scarcely longer than the lower jaw and are approximately 15 and 18% of the body length respectively. The cross-section of this bill is more circular than in Recent *Tetrapturus* and *Istiophorus*: depth approximately 88% of width. I have not seen any other fossil *Tetrapturus* or *Istiophorus*. Until better more, or better specimens are available, I follow Woodward's (1901) assessment that this bill is more circular than any other known *Istiophorus* (which is also more circular than any known *Tetrapturus*).

Gen. et sp. indet. *non Xiphiorhynchus* (Fig. 7.55)

Xiphiorhynchus parvus Casier, 1966: 314, pl. 51, fig. 5 (BMNH P21306).

Diagnosis. Billfish rostra without preserved generic or specific apomorphies.

BMNH P13713-7, Ameki, Ombialla District, Nigeria (Lutetian); P21306 (Holotype of *Xiphiorhynchus parvus*, Fig. 7.55), Sheppey, England, Early Eocene: Ypresian (London Clay). USNM 244484, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., rostrums, Early Pliocene: Zanclean (Yorktown Formation); 53510, 6.4 km by road W of Post Office at a few hundreds of meters N of State Route 41, immediately W of Tuckahoe Church, Jones Co, North Carolina, U.S.A., Eocene? (Claibornain Castle Hayne Formation).

Description. *Xiphiorhynchus parvus* is based on a small rostrum which is almost circular in cross-section, striated dorsally, ventral patch of villiform teeth, and two large nutrient canals. *Xiphiorhynchus* characterised by four nutrient canals. USNM 244484 is labelled *Makaira homalorhamphus*. This most probably refers to *Istiophorus homalorhamphus* Cope, 1869. *I. homalorhamphus* is based on an enigmatic specimen, which has also been thought to be a *Tetrapturus* (see Schultz,

1987). USNM 244484 is a rather well preserved billfish rostrum, ovoid in transverse cross-section, both prenasals well visible in dorsal aspect, two nutrient canals and a suture in sagittal plane. This specimen could belong to any Istiophorini-genus except *Istiophorus*, which has no median suture in bill.

Genus **indet.** ***non Cylindracanthus?*** (Fig. 7.56)

Cylindracantus rectus White, 1926: 70, pl. 18, figs. 1-5 (probably *non Coelorhynchus rectus*Dixon, 1850).

Diagnosis. Strongly constricted elongated centra.
Referred material. BMNH P13713-7, Ameki, Ombialla District, Nigeria (Lutetian).
Description A few billfish-like centrums (Fig. 7.56a) which agree with the above given diagnosis. A few other, considerably larger and not billfish-like (Fig. 7.56b).
Remarks. White (1926) described the specimens discussed here as *Cylindracanthus.* I do not doubt that the constricted, elongated centrums are of billfish and indeed, istiophorins. However, small istiophorin-like centra cannot be assigned to *Cylindracanthus. Cylindracanthus* is a genus only positively known from spines, which are normally associated with rostra of "blochiids" (see Casier, 1966; Schultz, 1987). I argue further up that these spines should not be recognised as billfish. Centra described under the name *Cylindracanthus* are not known to have been found associated with *Cylindracanthus* spines.

Gen. et sp. **indet.** ***non Istiophorus*** (Fig. 7.57)

Diagnosis. Ovoid centrum, two nutrient canals.
Referred material. USNM 498678 (Fig. 7.57) & 498681-498683, (formerly lumped together in "Lot 21"), Aurora, Lee Creek Mine, North Carolina, U.S.A., Miocene (Fish Stratigraphic Column, Pungo River Formation).
Description. Ovoid rostra. Prenasals well preserved. Premaxillae with numerous rows of minute conical teeth. Ventrally a symphysis between premaxillae, unfused along most of length of rostrum. Transverse cross-section shows two nutrient canals. Median suture badly discernible.
Remark. The presence of the median suture reveals that this is not an *Istiophorus*, but based on these fossils I cannot conclude whether they belong to *Tetrapturus* or *Makaira.*

Tribe **Palaeorhynchini** Günther, 1880

An extinct family of billfishes, characterised by a large number of vertebrae (around 45-60), neural and haemal spines modified with an ovoid plate like extension throughout most of vertebral column, or modified into parallellogram-shaped plates as in istiophorins, and modified into a laterally flattened fan-shaped structure on preural vertebrae (see also Chapter 5). The modified spines of preural vertebrae have been seen in a new genus, described below and in *Palaeorhynchus*. In other palaeorhynchin genera, this character is treated as either uncertain or missing (e.g. if the caudal region was not preserved) in the cladistic analysis. The hypural plate consists of all five hypurals, a hypural notch is present, and the parhypural is fused with the plate. In specimens where the tail is preserved, there is always hypurostegy. There is one continuous dorsal fin, consisting of soft rays. Palaeorhynchins existed throughout the whole of the Eocene.

Genus *Makairoides* gen. nov.

Etymology. Name based on resemblance of axial skeleton to *Makaira*.
Diagnosis. Enlarged, parallellogram-shaped neural and haemal spines, preural neural and haemal spines straight and apically widened into fan-shape.
Type species. The type species is described below.
Species composition. Only one species known, described below.

Makairoides melitensis sp. nov. (Fig. 7.58)

Etymology. Species named after the location of origin: Malta.
Diagnosis. As for genus.
Referred specimens. BMNH P6206 (Fig. 7.58), **holotype**, Malta, Early-Middle Miocene: Burdigalian-Landinian, vertebrate beds of *Globigerina* Limestone).
Description. Specimen contains only caudal section of vertebral column of a billfish. The 13 (including urostyle) most caudal vertebrae and fragment of hypural plate are preserved. Centrums slightly longer than deep: two centrums measured, both of which are 29 mm deep, while one is 34 and another 36 mm long; medially slightly constricted. Prezygapophyses strongly enlarged, seemingly enclosing preceding neural and haemal spines, as in istiophorins (Fig. 5.28c). Neural and haemal spines badly preserved, but apparently shaped as in istiohorids, which have enlarged, plate-like, parallellogram-shaped neural and haemal spines. Condition in *Makairoides* resembles most that of Recent istiophorin *Makaira*, whose neural and haemal spines are larger than those of *Istiophorus* and *Makaira* and also placed under a more obtuse angle to the centrum than those in *Istiophorus* and

Tetrapturus. Preural centra 3-7, on the other hand, have neural and haemal spines, which originate relatively posteriorly from centrum, are placed in (almost) straight angle towards centrum, are laterally compressed and widened along axis of vertebral column. Apically, these spines widen, to create flat fan-shaped structure. Hypural plate too badly damaged to report details.

Remarks. This fossil displays a peculiar mix of characters. The modified neural and haemal spines (except those of the preural centra) and prezygapophyses are normally seen as istiophorin synapomorphies. The centra of istiophorins, however, are medially strongly constricted and much more elongated (Fig. 5.28c). Because of the fan-shaped preural spines, *Makairoides* is included with the palaeorhynchins, and because of the parallelogram-shaped spines, forms a link between istiophorins and other palaeorhynchins.

Genus *Homorhynchus* Van Beneden, 1873

Histiophorus Agassiz, 1833-44: pl. 30 (figure only, *non* Cuvier, 1832)

Palaeorhynchum Agassiz, *l.c.*: 80, 85, Plate 32, fig. 1; Plate 34a, fig. 1 (*pro parte*, *non* De Blainville, 1818).

Hemirhynchus Agassiz, *l.c.*: 87 (*non* Hodson, 1843).

Homorhynchus Van Beneden, 1873: 210.

Diagnosis. Upper and lower jaw of different length: upper jaw developed into long rostrum, lower jaw not remarkable elongated. Number of dorsal fin rays about double amount of vertebrae.

Type species. *Homorhynchus deshayesi* (Agassiz, 1844).

Species composition. Two species are known: *H. deshayesi* from the Middle Eocene of France and *Homorhynchus colei* (Agassiz, 1844) from the Early Oligocene of Switzerland and the Caucasus region in Russia. *H. colei* is described below.

Homorhynchus colei (Agassiz, 1844) (Fig. 7.59)

Palaeorhynchum colei Agassiz, *l.c.*: 85, pl. 32, fig. 1.

Palaeorhynchum microspondylum Agassiz, *l.c.*: 85, pl. 34a, fig. 2.

Hemirhynchus colei Wettstein, 1886: 78.

Homorhynchus colei Danil'chenko, 1960: 161, pl. XV, fig. 2.

Diagnosis. As for genus. I have not seen specimens of the other *Homorhynchus* species, *H. deshayesi*, hence it is not discussed here.

Referred specimens. PIN 1413-5, 3363-134 (Fig. 7.59) and 3363-135, river Belaya, Caucasus, Russia, Early Oligocene: Rupelian (Khadum deposits).

Description. A detailed description is given by Danil'chenko (1960). Additional information and different observations are given here. lachrymal small, shorter than orbit diameter. Supratemporal groove short. Pterotic spine short. Ceratohyal without ventral projections. Total number of vertebrae 55, 53 according to Danil'chenko. Centra medially constricted, but not as extremely as in istiophorins. Plate-like extension of neural and haemal spines narrow and almost spine-like, whereas ovoid and more plate-like in *Palaeorhynchus* (see also Chapter 5 and description of *Palaeorhynchus*). Caudal fin hypurostegic, with widened and widely spaced medial lepidotrichia and a total of 31 lepidotrichia. Procurrent spur absent. Pectoral fin with 18 rays. Dorsal fin with (97?-) 107-108 tightly packed (more than one per interneural space) soft rays.

Remarks. *Palaeorhynchum egertoni* Agassiz, 1844 is sometimes mentioned in the synonymy of *H. colei* (Woodward, 1901; Danil'chenko, 1960). However, based on the Figure of *Palaeorhynchum egertoni* (Agassiz, 1833-44: Plate 34a, Fig. 1) it is impossible to say if "*H. egertoni*" and *H. colei* are identical. Wettstein (1886) suspected that they are, but that additional and better material is needed to confirm this. If *H. egertoni* and *H. colei* are found to be identical, then the first mentioned should be preferred, since the epithet *egertoni* appears on page 80 of Agassiz' (1833-44) monograph, while *colei* appears on page 85.

Genus ***Palaeorhynchus*** De Blainville, 1818

Palaeorhynchum De Blainville, 1818: 314.

Palaeorphynchum Winkler, 1867: 632 (*err. typ.*).

Hemirhynchus Kramberger-Gorjanović, 1879: 59, pl. xv, fig. 1 (*non* Agassiz, 1844).

Diagnosis. Upper and lower jaw straight, elongated, of equal length or almost (Fig. 7.60a), vertebrae 50-60 in number. *Pseudotetrapturus* also has jaws of equal length but these are slightly curved, and it has only 45-50 vertebrae. Dorsal fin elements about as numerous as vertebrae. In *Homorhynchus* the amount of dorsal elements is about double the number of vertebrae.

Type species. *Palaeorhynchus glarisianus* De Blainville, 1818.

Species composition. Nine species are known, found from the Upper Eocene to Lower Miocene sediments. Below follow descriptions of *P. glarisianus* and *Palaeorhynchus parini* Bannikov, 1992. *Palaeorhynchus senectus* Danil'chenko, 1962 is here described as Palaeorhynchinae indet.

Remarks. Specimen PIN 1413-79, labelled to be the holotype of *Palaeorhynchus crios* is nowhere referred to. It concerns a billfish with an elongated lower jaw, and an incomplete postcranial skeleton. It does not seem to possess apomorphies on the basis of which I can classify the specimen.

Palaeorhynchus glarisianus De Blainville, 1818 (Fig. 7.60)

Palaeorhynchum glarisianum De Blainville, 1818: 314. Type loc: Glarus, Switzerland, Oligocene

Palaeorhynchum latum Agassiz, 1833-44: 82, pl. 32, fig. 2; Pls. 35, 36. Type loc. *ibid.*

Palaeorhynchum medium Agassiz, 1833-44: 84, pl. 33. Type loc. *ibid.*

Palaeorphynchum sp. de Glarus Winkler, 1867: 632 (*err. typ.*?).

Palaeorhynchus glaronensis Wettstein, 1886: 73, figs. 14-16. Type loc. *ibid.*

Diagnosis. Vertebrae 60 in total, between 30 and 35 caudal vertebrae. *P. parini* also has 60 vertebrae, with 37 caudal vertebrae. Most other *Palaeorhynchus* seem to have less than 60 vertebrae.

Referred specimens. BMNH 41815 (Fig. 7.60a), 41818 (Fig. 7.60c), P1551 (Fig. 7.60b) P1714, Engi, Canton Glarus, Switzerland, Early Oligocene: Rupelian (Glarnerschiefers).

Description. The most detailed description of this species is given by Wettstein (1886). Additional observations are noted here. Slender, almost snake-like fish (Fig. 7.60c). Supratemporal groove not extending over whole length of frontal. Bill appears to be dorsolventrally flattened, but this is probably an artefact of fossilisation. In specimens of *P. parini* the bill appears to be ovoid in cross-section. Total number of vertebrae 60. Exact number of caudal vertebrae sometimes difficult to verify, but number ranges between 30 and 35 (Wettstein stated that 33-36 vertebrae belonged to the tail. I am uncertain whether he refers to the caudal vertebrae here). *Palaeorhynchus parini*, probably a closely related species has 37 caudal vertebrae. Neural and haemal spines modified, with distal, ovoid plate-like extension. Plate-like extensions sometimes obscured in badly preserved fossils from the Oligocene black slate from Switzerland. The plate-like extensions can be seen under high maginifcation, even if there is not much relief in specimen. Caudal fin hypurostegic (Fig. 7.60c) and with enlarged and widely spaced median lepidotrichia. First dorsal pterygiophore inserted in third interneural space. I could not make proper dorsal fin-ray counts on specimens, but there seems to be only one pterygiophore inserted per interneural space, but from the 14th preural vertebra on there are two pterygiophores per interneural space. First anal pterygiophore inserted in the 13th interhaemal space anterior of first haemal spine (starts at eighth or ninth pair of ribs according to Wettstein). First 14 anal fin rays appear to be stiffer and rigid than subsequent rays. Wettstein mentioned that the anterior tail fin ends at the 17th preural vertebra. This puzzling description might mean that Wettstein counted this section of stiffer rays as a separate element, with its last spine at the 17th preural vertebra. However, I interpret these more rigid rays as soft rays and not as spines, which is in accordance with my observations in *P. parini*. Bannikov (1993b) also did not recognise the presence of anal fin spines in

Palaeorhynchus. Total number of anal fin rays 59-62. Body covered by small scales.

Palaeorhynchus parini Bannikov, 1992 (Fig. 7.61)

Palaeorhynchus parini Bannikov, 1992: 28, figs. 1-3 (I have used translation: Bannikov (1993b): 51, figs. 1-3).

Diagnosis. Vertebrae 60 in total, of which 37 caudal. *P. glarisianus* also has 60 vertebrae, of which 30-35 are caudal.

Referred specimens. PIN 4425-13, **(holotype**, Fig. 7.61), 4425-14 **(paratype)**, 4425-15 and 4425-16 river Pshekha, left bank, 1 km upstream of Gornyy Luch village, Caucasus, Russia, Middle Eocene (Bartonian, Kuma Horizon).

Description. A detailed description is given by Bannikov (1993b). Different and additional observations are given here. Supratemporal groove not extending over whole length of frontal. Bill appears to be ovoid in cross-section. Total number of vertebrae 60, of which 37 caudal. Dorsal fin with in total 71 (54+17) rays (50-51+17 according to Bannikov). Caudal fin with enlarged and widely spaced median lepidotrichia. Pelvic bones small according to Bannikov, but I think that due to relatively poor conservation of fossil, correct shape and size of pelvic bone cannot be assessed. Pelvic with 5-6 rays according to Bannikov. I believe there are five soft rays without a spine.

Genus ***Pseudotetrapturus*** Danil'chenko, 1960

Pseudotetrapturus Danil'chenko, 1960: 162, pl. XXIII, figs. 1, 2.

Diagnosis. Lower jaw almost as long as upper jaw, 45-50 vertebrae. Scales large. Another genus with an elongated lower jaw is *Palaeorhynchus*, which has 50-60 vertebrae and straight jaws, whereas the jaws of *Pseudotetrapturus* are curved at the tips (Fig. 7.62).

Type species. Only one species known, described below.

Species composition. Only the type species.

Pseudotetrapturus luteus Danil'chenko, 1960 (Fig. 7.62)

Pseudotetrapturus luteus Danil'chenko, 1960: 162, pl. XXIII, figs. 1, 2. Type loc. River Sulak, Russia, Eocene.

Diagnosis. As for genus.

Referred specimens. PIN 1413-50 (**holotype**) and 1413-51, river Sulak, Caucasus, Russia, Late Eocene: Priabonian (Riki Horizon).

Description. A detailed description is given in Danil'chenko (1960). Additional information and different observations are noted here. Supratemporal groove short. Postero-superior fossa behind middle of orbit. Pterotic spine short. Vertebrae constricted, but not as radically as in istiophorins. Large scales, observed on gill cover only (Fig. 7.62a). According to Danil'chenko (1960) they cover whole body. In cladistic analysis, scale covering treated as uncertainty between anterior corselet and complete scale covering. However, *Pseudotetrapturus* is unlikely to have anterior corselet, as this never occurs in billfishes. I am uncertain what Danil'chenko means when he states that the neurapophyses have flattened processes. Although badly preserved, neural and haemal spines have enlarged plate-like extensions, as seen in *Palaeorhynchus* and *Homorhynchus* (see Fig. 7.62b). It might be that these are Danil'chenko's modified neurapophyses. Vertebrae could not be counted in studied specimens. According to Danil'chenko there are between 45 and 50.

Gen. et sp. **indet. 1** (Fig. 7.63)

Palaeorhynchus senectus Danil'chenko, 1962: 123, fig. 11. Type loc. Tbilisi, Georgia, Eocene.

Diagnosis. Head relatively deep, teeth clearly visible.

Referred material. PIN 1413-80 (**holotype** of *Palaeorhynchus senectus*, Fig. 7.63), Tbilisi, Georgia, Middle Eocene (Dabakhansk Svita).

Description. Described as *Palaeorhynchus senectus* in Danil'chenko (1962).

Remarks. *Palaeorhynchus senectus* is described from a poorly preserved specimen: the anterior region of what appears to be a palaeorhynchin-like fish (Fig. 7.63). Both upper and lower jaw are elongated and straight. This means that the specimen is not a *Pseudotetrapturus*, which has jaws that are curved at the tips. I consider straight jaws, seen in all billfish but *Pseudotetrapturus*, as a plesiomorphy, which means that *P. senectus* does not necessarily have to be a *Palaeorhynchus*: it could be another palaeorhynchin with plesiomorphous straight jaws. Even if "*P. senectus*" is a *Palaeorhynchus*, it cannot be specified. Bannikov (1993b) stated that *P. parini* can be identified from *P. senectus* because the latter has a deeper head. However, "*P. senectus*", much smaller than *P. parini*, is probably at an earlier ontogenetic stage, which means that the deeper head might not be a character for species division, but an indication of the ontogenetic stage. This seems to be confirmed by the presence of, for palaeorhynchins, relatively large teeth. They are clearly visible in the fossil, whereas they are mostly hard to find in palaeorhynchin fossils. The holotype of *P. senectus* does not seem to possess any

specific apomorphies. I think it better to describe this specimen as Palaeorhynchini indet.

Genus and species indet. 2

Palaeorhynchus zitteli Danil'chenko 1960: 159, pl. XV, fig. 1 (*pro parte*).

Diagnosis. Rounded forehead.
Referred specimen. PIN 1413-49, river Belaya, Caucasus, Russia, Early Oligocene: Rupelian (Upper/Middle Khadum deposits).
Description. PIN 1413-49 is the skull of a palaeorhynchin-like fish, used as part of the material for Danil'chenko's (1960) description of *Palaeorhynchus zitteli*, which is otherwise known from Rajcza (Carpathian region) and Galicia, Spain (Woodward, 1901).
Remarks. Not having seen other specimens of *P. zitteli*, I cannot state anything on the validity of that genus. It is said to have a deeper body than *P. glarisianus* (see Woodward, 1901) and less vertebrae (Danil'chenko, 1960). However, since the referred specimen is a head only, these characters cannot be assessed. The head of this "*P. zitteli*" does not appear to be significantly deeper than those of *P. glarisianus*, although with the state of preservation of the fossils this is not easy to assess. The rounded forehead of this specimen is also seen in the so-called *P. senectus*, whose identity is mysterious to me: "*P. senectus*" is described above as Palaeorhynchinae *Genus and species* indet. While *P. zitteli* might be a valid species, I think it is better not to assign PIN1413-49 to a known species.

Tribe **unknown**

Genus *Rotundorhynchus* gen. nov.

Etymology. *Rotundorhynchus* literally means "roundsnout" in Latin.
Diagnosis. Transverse cross section of bill almost circular or slightly ovoid, deeper than bill of *Xiphiorhynchus*. One large central canal extending to almost anterior tip of rostrum, two lateral nutrient canals.
Type species. Only one species known, described below.
Species composition. Only the type species.
Remarks. *Rotundorhynchus* shows an interesting mix of characters. A central canal that extends far anteriorly is known from *Xiphiorhynchus*. The possession of one pair of nutrient canals is a feature of istiophorins.

Rotundorhynchus brittanicus sp. nov. (Fig. 7.64)

Etymology. Species named after country of origin of only known specimens.
Diagnosis. As for genus.
Holotype. BMNH P1765, Sheppey, England, Early Eocene: Ypresian (London Clay).
Referred material. The holotype and BMNH P23838, Sheppey, England, Early Eocene: Ypresian (London Clay).
Description. Holotype has been cut in two halves, perhaps during original preparation work of specimen (Fig. 7.64a). Sagittal cross-section of this specimen reveals that central nutrient canal almost reaches anterior tip of bill. Ventral side with multiple rows of minute teeth. Teeth missing, but sockets preserved (Fig. 7.64a). Dorsal surface rugose (Fig. 7.64b). Transverse cross-section of holotype almost circular, of paratype more ovoid (Fig. 7.64c). One central canal, two rather large nutrient canals, one of which is preserved in paratype (Fig. 7.64).

Scombridae Tribe *incertae sedis*

Genus *Eocoelopoma* Woodward, 1901

Coelopoma Agassiz 1833-44: 139; Agassiz, 1845: 307 (*nomina nuda*).

Eocoelopoma Woodward, 1901: 470.

Diagnosis. Fossae for lateral muscles of the trunk (postero-superior fossa) more anteriorly placed than in other scombrids: near middle of the of orbit (Fig. 5.2a). Part of frontal anterior of postero-superior fossa, thickened and ornamented with more or less fine lines.
Type species. *Eocoelopoma colei* Woodward, 1901.
Species composition. *Eocoelopoma curvatum* (Owen, 1854), *E. colei* and *Eocoelopoma gigas* Casier, 1966 from England and *Eocoelopoma portentosa* Bannikov, 1985 from Turkmenistan, all of Ypresian age. *Eocoelopoma* teeth of the Palaeocene of Equatorial Africa are also mentioned (Bannikov, 1985).
Remarks. *Eocoelopoma hopwoodi* Casier, 1966 is now considered a species belonging to a new genus (see below).

Eocoelopoma colei Woodward, 1901 (Fig. 7.65)

Coelopoma colei Agassiz, 1833-44,: 139; Agassiz, 1845: 307 (*nomina nuda*).

Scombrinus nuchalis Woodward, 1901: 462 (*pro parte*).

Eocoelopoma colei Woodward, 1901: 470. Type loc. Sheppey, England, Eocene.

Diagnosis. Opercular bones, especially preoperculum, ornamented with clearly visible irregular wrinkles (as opposed to relatively smooth opercular bones in other species) and frontals ornamented with relatively widely spaced curved lines, less fine than in other species of *Eocoelopoma.*

Referred material. BMNH P623a **(holotype)**, P26702, P26805 and USNM 22388 (Fig. 7.65), Sheppey, England Early Eocene: Ypresian (London Clay); P12945, Southend-on-Sea, Essex, England, Early Eocene: Ypresian (London Clay).

Description. A description is given by Casier (1966). Additional information and observations differing from that description given here. Small skulls, almost as long as wide. Neurocranium length 55-83 mm, maximum width 46.5-76 mm. Supratemporal groove short, not extending rostrad to snout. Temporal groove posteriorly strongly depressed, anterior part of groove shallower (Fig. 7.65b). Postero-superior fossa reaching middle of orbit, near lateral margin of frontal. Anterior apex of frontal pointed. Pterotic a short, narrow, triangular wing. No posterior projection on intercalar. Anterior margin of vomer slightly protruding, with patch of villiform teeth. Palatine with numerous, minute, conical, retrorse teeth. Teeth relatively stout, straight, conical, about equal in size (2 mm) and a few mm apart to close together. Hyoidean window present.

Eocoelopoma curvatum Woodward, 1901 (Fig. 7.66)

Coelopoma laeve Agassiz, 1833-44: 139; Agassiz, 1845: 370 (*nomina nuda*).

Coelopoma curvatum Owen, 1854: 162 (*nomen nudum*).

Scombrinus nuchalis Woodward, 1901: 462 (*pro parte*).

Eocoelopoma colei, Woodward, 1901: 471 (*pro parte*).

Eocoelopoma curvatum Woodward, 1901: 472. Type loc. Sheppey, England, Eocene.

Diagnosis. Anterior part of frontal, anterior of postero-superior fossa, densely ornamented with fine, curved lines. Opercular bones smooth.

Referred material. BMNH 24613 (Fig. 7.66b, c), P4151, P9455 (Fig. 7.66a), P9456a, P26714 (formerly P1698c from Woodward, 1901) and USNM 22389, Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. Previous description given by Casier (1966). Different observations and additional information is given here. Sizes variable, but generally not very large. Cranium short and broad, only about 1.7 times longer than wide. BMNH 24613, P4151 and USNM 22389: 80 mm long, BMNH P26714 more than 80 mm long, but unable to measure whole length. Maximum width frontals 29-71 mm. Anterior margin of frontal rather blunt and rounded. Postero-superior fossa

somewhat posterior of middle of orbit (Fig. 7.66b). Anterior part of temporal groove shallow, posterior part strongly depressed, thus resembling a large fossa (Fig. 7.66b). Apex of epiotic with a flat, short projection pointing laterally. Pterotic a short wing. Intercalar without distal projection. Parasphenoid straight in lateral view and slightly oblique: slanted in ventral direction caudally. Palatine with minute sharp, cuved teeth. Parasphenoid rather wide anteriorly, tapering posteriorly. Opercular bones rather smooth, only preoperculum with a slightly rugose ornamentation (Fig. 7.66a). Anterior ascending process of Premaxilla rather large but short. Teeth slender, smooth, ovoid, elongate and sharply pointed. About 3.5 mm long, almost all teeth of same size. Right dentary of BMNH P9455 possesses at least 15 teeth which are a few mm apart. Eye sclerotics rather large (diameter 27 mm), clearly bulging laterally. Lachrymal large, longer than orbit diameter. Hyoidean window not observed. Ventral margin of ceratohyal with ventral projections. Opercular bones covered with scales with a maximum diameter of 3.5 mm. In BMNH P4151, first six vertebrae preserved. Centrum about as long as deep and wider than deep. Second centrum 6 mm long and deep.

Eocoelopoma gigas Casier, 1966 (Fig. 7.67)

Eocoelopoma colei Woodward: 471 (*pro parte*, BMNH 33305)

Eocoelopoma gigas Casier, 1966: 281, pl. 45. Type loc. Sheppey, England, Eocene.

Diagnosis. Larger species than others: length between hind margin of preoperculum and snout 220 mm (BMNH 39221, cranium of other species between 55 and 135 mm). Opercular bones smooth (Fig. 7.67a), small area of not so dense ornamentation rostral of postero-superior fossa.

Referred material. BMNH 39221 (**holotype**, Fig. 7.67a) and BMNH 33305 (Fig. 7.67b-d), Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. A description is given in Casier (1966). Different observationns and addtional information given here. Postero-superior fossa somewhat anterior of middle of orbit, close to lateral margin of frontal (Fig. 7.67b, c). Anterior of postero-superior fossa, frontal thickened. Hinder part of this thickened region lightly ornamented with fine curved lines (Fig. 7.67c). Apex of epiotic with a flat, short projection pointing laterally. Parasphenoid straight in lateral view. Anterior margin of vomer diamond-shaped and strongly protruding ateriorly (Fig. 7.67d). Opercular bones rather smooth, only Preoperculum with a slightly rugose ornamentation. Teeth slender, smooth (slightly striated basally), ovoid, elongate and sharp-pointed, about 6 mm long, almost all teeth of the same size.

Eocoelopoma portentosa Bannikov, 1985 (Figs. 7.68, 7.69)

Eocoelopoma portentosa Bannikov, 1985: 41, figs. 18-20a, pl. IV, fig. 6, pl. V, fig. 1. Type loc. Uilya-Kushlyuk, Turkmenistan, Eocene.

Diagnosis. Differs from other *Eocoelopoma* by the following unique combination of characters: longer jaws: posterior end of upper jaw extending caudally beyond halfway the orbit: an autapomorphy of this species within scombrids (not reaching hind margin of orbit, as Bannikov, 1985 suggested), premaxilla with larger ascending process, dentary with a chin-like symphysial process (Fig. 7.68a, 7.69) and preoperculum with relatively straight anterior margin.

Referred specimen. PIN 1762-85 (**holotype**, Figs. 7.68, 7.69), Uilya-Kushlyuk village, Turkmenistan, Ypresian (Middle Danatinsk Svita).

Description. Detailed description given by Bannikov (1985). Different observations and additional information noted here. Cranium 77 mm long. Frontal short and broad. Postero-superior fossa almost reaching middle of orbit, contrary to Bannikov's (1985) description that suggests it reaches beyond the middle (Figs 7.68, 7.69). Possesses depression anterior of supraoccipital, but this seems to be an artefact of fossilisation and no pineal window. Depresseion orientated across frontals, not alongside axis as in pineal window. Pterotic spine short. Teeth slender, smooth, elongate and sharply pointed. About 4 mm long, most teeth of the same size. Right premaxilla with about 19 (18-20 *sensu* Bannikov) teeth, each a few mm apart. Lachrymal not well preserved, but smaller than length of orbit. (Figs. 7.68a, 7.69). Bannikov (1985) mentions that the species has 40 vertebrae. His figure (Bannikov, 1985, fig. 18a) suggests that, including the urostyle, *E. portentosa* has 39 vertebrae. I do not know where these figures are based on, as the holotype does not contain all vertebrae. All other specimens known of the species (Bannikov, 1985) are skull fragments. Caudal skeleton with hypural plate, which is fusion of urostyle, uroneural, parhypural and hypurals 1-5. Hind margin of plate has small vestigial remnant of caudal notch (not observed by Bannikov). Tail fin damaged, but probably semilunate. Lepidotrichia leave marks of hypurostegy on hypural plate. Pelvic fins I spine and 5 soft rays. First dorsal pterygiophore inserted in 3rd (5th-6th according to Bannikov) interhaemal space. Bannikov (1985) mentions that *Eocoelopoma* has adjoining dorsal fins, but this cannot be seen in the holotype, which is also suggested by the figure (Bannikov, 1985, fig. 18a). Anal fin: II spines followed by 9 (9-10 according to Bannikov) soft rays, and 9 (7-8, according to Bannikov) anal finlets.

***Eocoelopoma* sp.**

Referred material. One Tooth, BMNH P29983, Bognor, Sussex, England, Early Eocene: Ypresian (London Clay, Lower Fish Tooth Bed) and a damaged skull, BMNH P26706 (labelled as *Eocolopoma curvatum*), Sheppey, England, Early Eocene: Ypresian (London Clay).

Description and remarks. BMNH P29983: clearly an *Eocoelopoma* tooth: slender, smooth (barely striated basally), ovoid, elongate, sharply pointed and slightly bent to the axial? side. About 4 mm long. Specific identity cannot be determined, bur seemingly too small to be *E. gigas*. BMNH P26706: damaged neurocranium with the anterior part of frontals missing. Clearly an *Eocoelopoma*, through pattern of ridges and dents on skull roof and anteriorly placed postero-superior fossa. Skull too small to be *E. gigas*. Could be either *E. colei* or *E. curvatum*, but apomorphies that would identify either missing. Specimen labelled as *E. curvatum*, but nowhere documented.

Genus *Tamesichthys* Casier, 1966

Tamesichthys Casier 1966: 271, pl. 40, fig. 1.

Diagnosis. Lower jaw protrudes upper jaw, large scales on opercular bones.

Type species. Only one species known, described below.

Species composition. Only the type species.

Tamesichthys decipiens Casier, 1966 (Fig. 6.70)

Tamesichthys decipiens Casier, 1966: 271, pl. 40, fig. 1. Type loc. Sheppey, England, Eocene.

Diagnosis. As for genus.

Referred material. BMNH 41319 (**holotype**, Fig. 6.70), Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. A detailed description is given by Casier (1966). To that description I can only add that the lower jaw protrudes the upper jaw.

Remarks. Based on its preserved characters it is not easy to assess the affinities of *Tamesichthys*. The protruding lower jaw is a characteristic of trichiurids, but *Tamesichthys* does not possess any fangs. The teeth are straight and not retrorse as in gempylins. Superficially, *Tamesichthys* somewhat resembles a generalised gempylin, but it does not possess all gempylin synapomorphies. *Tamesichthys* may have affinities with advanced scombrids, if the large scales on its opercular apparatus are remnants of an anterior corselet. The anterior margin of the

preoperculum forms a blunt angle, as in *Scomberomorus*, *Acanthocybium* and Sardinae. The operculum is deep and acutely tapered ventrally, as in the scombrins.

SCOMBROIDEI FAMILY *INCERTAE SEDIS*

Genus ***Duplexdens*** nov. gen.

Cybium Agassiz, 1835b: 42 (*nomen nudum*, *non* Cuvier, 1829).

Cybium Agassiz, 1833-44: 62, pl. xxvi, figs. 1-3 (*non* Cuvier, 1829).

Scombrinus Woodward, 1901: 463 (*pro parte, non l.c.*: 462).

Scombramphodon Woodward, 1901: 475 (*pro parte, non l.c.*: 474).

Acestrus Casier, 1966: 315, pl. 40, fig. 3 (*non* Woodward, 1901).

Etymology: *Duplexdens* literally means "double tooth" in Latin. An apomorphy of this genus is jaws with (incomplete) double tooth rows.

Diagnosis. Genus known from skull only. Length of lachrymal greater than maximum diameter of orbit, ethmoid anteriorly crescent-shaped, jaw teeth represented by two incomplete tooth rows.

Type species. One species known, described below.

Species composition. Type species only.

Remarks. The only species of *Duplexdens* was previously known as *Scombrinus macropomus* (Agassiz, 1844). This species is not congeneric with *Scombrinus*, which does not share *Duplexdens*' apomorphies of the double tooth rows and the emarginated anterior margin of the ethmoid. Since *Scombrinus nuchalis* is the type species of its genus, a new genus *Duplexdens* has been created for this species.

Duplexdens macropomus (Agassiz, 1844) comb. nov. (Fig. 7.71)

Cybium macropomum Agassiz, 1835b: 42 (*nomen nudum*).

Cybium macropomum Agassiz, 1833-44: 62, pl. 36. figs. 1-3. Type loc. Sheppey, England, Eocene.

Scombrinus macropomus Woodward, 1901: 463. Type loc. *ibid.*

Scombranphodon crassidens Woodward, 1901: 475 (*pro parte*, BMNH 28755).

Scombramphodon sheppeyensis Casier, 1966: 276, pl. 40, fig. 4. Type loc. *ibid.*

Acestrus elongatus Casier, 1966: 316, pl. 40, fig. 3. Type loc. *ibid.*

Diagnosis. as for genus.

Referred material BMNH 28755, (**holotype** of *Scombramphodon sheppeyensis*), 28758, 38907 (Fig. 7.71c), P158, P166, P12954 (**holotype** of *Acestrus elongatus*) and P4145 (Fig. 7.71a, b); GLAHM V2017 and V3470; Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. Neurocranium 122-140 mm long. Frontals coarsely ornamented with a rugosity of lines, most running parallel to axis of skull. Pineal window and frontoparietal fenestra absent. In some specimens, through damage, seemingly a large pineal window present (Fig. 7.71a). Supratemporal groove present and short, not extending to anterior tip of frontal. Postero-superior fossa situated towards hind margin of orbit. Epiotic triangular, pointing postero-laterally. Lachrymal damaged in specimens, but length clearly greater than maximum diameter of orbit (Fig. 7.71b). Pterotic a short spine. No caudal projection on intercalar. Upper jaw long, reaching hind margin of orbit. Presence or absence of supramaxilla not clear. Maxilla/premaxilla complex tightly bound, non-protrusible. Premaxilla long and stout, with a relatively short and small rostral ascending process, which ascends with angle of 40° with horizontal part of premaxilla. Ascending process in itself two-pronged (Fig. 7.71a), as in Scombrinae. Both upper and lower jaw slightly damaged, and with rugose horizontal striations, upper jaw seemingly protruding lower jaw slightly. Two types of teeth: inner row of larger, and outer row of smaller teeth (Fig. 7.71c). Outer tooth row not observed in anteriormost part of either dentary or premaxilla. Small, conical teeth, fraction of 1 mm long. Principal teeth stout but slender, all of about same length of 6 mm and a few mm apart. Teeth conical, ovoid, straight and slightly striated basally. Presence or absence of prenasal unclear. Rostral margin of ethmoid indented, semi-forked (Fig. 7.71a.), as in Scomberomorinae and *Scombramphodon*. Eye sclerotics surrounding somewhat ovoid area, long side of oval vertical, about 33 mm long (BMNH P4145). Operculum deep, ventrad reaching dorsal margin of dentary. Ventral margin of ceratohyal smooth, without projections.

aff. ***Duplexdens***

Referred material. BMNH 38903, Sheppey, England, Ypresian, London Clay.

Description. One pair of damaged premaxillae. Ascending processes and small horizontal portion of premaxillae and anteriormost fragments of maxillae present. Ascending process of premaxilla stout, ascending with angle of 35° with horizontal part of premaxilla. Ascending process two-pronged dorsally, but prongs not as pronounced as in *D. macropomus*. Ascending process also seems to be longer than in *Duplexdens*, resembling somewhat a premaxilla of a Scomberomorinae, although those have longer ascending processes. Tooth sockets circular.

Remarks. Resembles *Duplexdens* by the stout and relatively long ascending process, whch distally has two projections. However, the differentiation of those two processes is less pronounced than in *Duplexdens*. The teeth are circular. It is clear that the teeth of *Duplexdens* are conical, but it is not clear if those from this specimen are circular or slightly compressed.

Genus ***Micrornatus*** gen. nov (Fig. 7.72).

Eocoelopoma Casier, 1966: 284, text-fig. 65, pl. 44, fig. 3 (*non* Woodward, 1901).

Etymology. Skull is characterised by a few shallow lines of ornamentation (micro-ornatus), as opposed to the numerous, clearer lines that cover the anterior part of the frontals of the similar genus *Eocoelopoma*.

Diagnosis. Postero-superior fossa near middle of orbit, pineal window present, anterior margin of ethmoid emarginated, anterior part of frontal thickened and lightly ornamented with curved lines.

Type species. Only one species known, described below.

Species composition. Only the type species.

Remarks. *Micrornatus* superficially resembles *Eocoelopoma*, hence it was described as part of that genus by Casier (1966). However, close investigation revealed significant differences. The anterior margin of the ethmoid is not emarginated in *Eocolopoma*, but it is in *Micrornatus* (Fig. 7.72a). Some specimens of *Eocoelopoma* seem to possess a large pineal window, but specimens of the same species may not possess one. All apparent pineal windows in *Eocoelopoma* appear to be caused by breakages in the thin parts of the frontals. In *Micrornatus* however, the borders of the narrow pineal slit appear to be smooth and natural. The frontals of *Micrornatus* are much less densely ornamented than those of *Eocoelopoma*. The teeth of *Micrornatus* (see Fig. 7.72b) are slenderer and longer than those of *Eocoelopoma*.

Micrornatus hopwoodi comb. nov. (Fig. 7.72)

Eocoelopoma hopwoodi Casier, 1966: 284, text-fig. 65, pl. 44, fig. 3. Type loc. Sheppey, England, Eocene.

Diagnosis. As for genus.

Referred material. BMNH 36136 (**holotype** of *Eocoelopoma hopwoodi*, Fig. 7.72), Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. See description of *Eocoelopoma hopwoodi* (Casier, 1966). Holotype is pictured in Fig. 7.72.

Genus ***Scombramphodon*** Woodward, 1901

Amphodon Storms, 1887: 265, pl. iv (*non Amphodus* Peters, 1872).

Scombramphodon Woodward, 1901: 474.

Diagnosis. Anterior margin of ethmoid emarginated. Complete double tooth row with teeth of outer tooth row smaller than those of inner row. Differs from similar genus *Duplexdens*, which has an incomplete outer tooth row and a wider skull.
Type species. Scombramphodon benedeni (Storms, 1887)
Species composition. Three species are recognised: *S. benedeni* and *Scombramphodon curvidens* (Storms, 1887) from the Rupelian (Early Oligocene) of Belgium and *Scombramphodon crassidens* Woodward, 1901 from London Clay sediments. *Scombramphodon sheppeyensis* Casier, 1966 is here described as a species belonging to a new genus *Duplexdens*, because it has an incomplete rather than a complete double tooth row. *Scombramphodon* has two complete tooth rows, of which the outer tooth row contains teeth much smaller than those of the inner tooth row. The holotype of *Scombramphodon woodwardi* White, 1926 (BMNH P11853α, β) suggests that both its tooth rows contained teeth of approximately the same size. The fossil is too poorly preserved to supply another possible identification. *S. crassidens* is described below.

Scombramphodon crassidens Woodward, 1901 (Fig. 7.73)

Sphyraenodus crassidens Agassiz, 1833-44: 99 (*nomen nudum*).

Dictyodus? crassidens Woodward, 1890: 64 (*nomen nudum*).

Scombramphodon crassidens Woodward, 1901: 475. Type loc. Sheppey, England, Eocene.

Diagnosis. As for genus. Other species of this genus have not been studied for comparison.
Referred material. BMNH P1763 (Fig. 7.73) and P65644 Sheppey, England, Early Eocene: Ypresian (London Clay).
Description. A detailed description is given by Casier (1966). Recently, a new specimen (BMNH P65644) has been discovered, which is more complete than any other *S. crassidens* specimen and well articulated (Fig. 7.73). The most significant new information contained in that specimen are the well preserved premaxillae, which possess complete double tooth rows (Fig. 7.73c), just as in the dentaries.
Remarks Two of Woodward's (1901) syntypes of *S. crassidens* (BMNH 38907 and P158) are described above as *Duplexdens macropomus.*

Genus ***Sphyraenodus*** Agassiz, 1844

Sphyraenodus Agassiz, 1833-44: 98, pl. 26, figs. 4-6.

Dictyodus, Woodward, 1890: 64 (*non* Owen, 1839).

Diagnosis. Unique combination of characters: conical teeth, slightly oval and with basal striations, post-temporal fossae (see description of *S. priscus*, below). Preserved precaudal part of trunk with large scales.

Type species. *Sphyraenodus priscus* Agassiz, 1844.

Species composition. The only species I managed to study is the type species. Four other species are found from the Thanethian up to the Oligocene, in Morocco, Belgium annd Germany. *Sphyraenodus goniopleurus* (Casier, 1966: 35 and index) is a misprint of *Myliobatis goniopleurus* Agassiz, 1834. Woodward (1901) noted that *Sphyraenodus conoideus* Von Meyer 1846 resembled a *Stereodus* Owen, 1865. However, a figured specimen in Von Meyer (1851) does not really compare with *Stereodus*. The shapes of their teeth at the base is different: *Stereodus* teeth are more circular and their density in the dentary is also less. "*S. conoideus*" does not seem to be a *Sphyraenodus* either. The base of a *Sphyraenodus* tooth is shaped differently and is striated, whereas the "*S. conoideus*" tooth is not. I have not been able to determine the identity of that fossil.

Remarks. Owen (1839) published a genus *Dictyodus*, based on fragmentary jaws. The name *Sphyraenodus* was published in 1839 for a figured specimen in the volume of plates belonging to the text of Agassiz' Recherches sur les Poissons Fossiles, volume V. The text volume, with the description of *Sphyraenodus* did not appear until 1844 (Agassiz, 1833-44). Later, (Owen, 1840-5), the section concerned was published in 1841) stated that *Dictyodus* was a synonym of *Sphyraenodus*. However, in this case, the name *Dictyodus* should have had age preference over *Sphyraenodus*. The name *Sphyraenodus* was not validly publised in 1839, being only a figure. It was validly published in 1844, as it was described then. It seems that Owen's *Dictyodus* was based on some fragmentary jaws in the Royal College of Surgeons. The specimens show a resemblance to *Sphyraenodus* (Woodward, 1901), but they are too imperfect for a definite determination. Hence it is not possible to employ the name *Dictyodus*, and the next valid name *Sphyraenodus* is retained.

Sphyraenodus priscus Agassiz, 1844 (Fig. 7.74)

Sphyraenodus priscus, Agassiz, 1833-44: 98, pl. 26, figs. 4-6. Type loc. Sheppey, England, Eocene.

Dyctiodus priscus Woodward, 1890 #345: 64. Type loc. *ibid.*

Diagnosis. As for genus.

Referred material. Skulls: BMNH 35106 (Fig. 7.74a, b), P3957 (**holotype**, Fig. 7.74c), P21651-54 (Fig. 7.74d), P25386-46, part of P21669 (scales only); Sheppey, England, Early Eocene: Ypresian (London Clay).
Description. Detailed description given by Casier (1966). Different observations and additional information given here. Teeth about equal in size. Eye sclerotics thick, with combined diameter about 25% of total length of neurocranium. Hyoid complex long and elongate. Hypohyal small, 17 mm long, ceratohyal (95 mm) long (measurements from holotype). Pelvic plate large, but not well preserved in specimens.
Remarks. Casier (1966, p. 287) figured a reconstruction of the neurocranium, with large posttemporal fossae, at the junction of the sphenotic, pterotic and the parietal. The presence of these fossae is an autapomorphy of *Sphyraenodus*. From the specimens (BMNH 35106, Fig. 7.74b), its exact size, shape and depth cannot (yet) be determined. It may be that these are not genuine fossae, but depressed parts of the temporal groove. The samples of loose teeth mentioned here (BMNH P21651-54 and P25386-46) are in the collection labelled "*Sphyraenodus* sp.". Casier (1966) described the differences in tooth morphology between the different species of *Sphyraenodus*, but did not describe the teeth of *Sphyraenodus rupeliensis*. The forementioned samples of loose teeth (Fig. 7.74d) seem to be identical to the *S. priscus* teeth. Only on the largest teeth, the striations seem a bit stronger than of those in the skulls P3957 and 35106. *S. rupeliensis* is only known from the Oligocene of Belgium (Leriche, 1910), while *S. priscus* is known from the Ypresian of England only. It is therefore likely that these teeth belong to *S. priscus*.

Sphyraenodus sp.

Diagnosis. Short, sharp conical teeth, dentary with chin-like projection.
Referred material. USNM 265382, Popes Creek, Bluff 1 mile S of, 1 ft above beach and 15 ft below gray Carbonaceous clay bed, Charles Co, Maryland, U.S.A., Ypresian (Pamunkey Group, Nanjemoy Formation).
Description. Dentary with almost complete dorsal dentigerous branch (93 mm long). About 10 tooth cavities are preserved, five of which contain teeth. Teeth short, about 6 mm tall, conical and sharp. Dentary shallow, preserved part of lower branch of dentary hardly sloping ventrad. Antero-ventral chin-like projection present.
Remarks. The specimen described above is labelled "*Sarda delheidi* Leriche". I have nowhere found a reference including this name. It is the most plausible that this is an unpublished synonym of *Eutrichiurides delheidi* (Leriche, 1908). *Eutrichiurides* possess a chin-like process, just as this fossil. Possibly based on

that *Sarda* also possesses such a "chin", tbe person labelling the specimen decided to label it as *Sarda delheidi*. However, this fossil fits in better with the diagnosis of *Sphyraenodus*. *Sphyraenodus* also has a chin-like projection, a slender dentary and short, sharp conical teeth. Having only studied specimens of *S. priscus*, I do not feel that I can make a proper diagnosis and comparisons with (other) species of *Sphyraenodus*. As far as I know, this is the first find of a *Sphyraenodus* in the U.S.A.

Genus ***Thyrsion*** Jordan, 1920

Thyrsites Jordan & Gilbert, 1919 (*non* Lesson, 1831)

Thyrsion Jordan in Jordan & Gilbert, 1920: 14.

Thyrsocles Jordan & Gilbert, 1920: 14.

Trossulus David, 1943: 150 (*pro parte*, *non* Jordan 1921).

Pneumatophorus David, 1943: 151 (*non* Jordan, 1833).

Diagnosis. Hypurals 1-4 fused. Number of vertebrae reaching more than 48.
Type species. One species known, see below.
Species composition. I recognise one species: *Thyrsion kriegeri* (Jordan & Gilbert, 1919). *Thyrsion velox* Jordan, 1920 is considered a junior synonym of *T. kriegeri* (see description of that species).

Remarks. Genus mostly known as *Thyrsocles*. Jordan described genus *Thyrsion* on his own, and genus *Thyrsocles* together with Gilbert in the same paper (Jordan & Gilbert, 1920). Later, Jordan & Gilbert (1921) acknowledge that *Thyrsion* and *Thyrsocles* represent the same genus. They state that *Thyrsocles* has page priority over *Thyrsion*, "being first printed in connection with a known species" and should thus be retained. The first printing of *Thyrsion* is on page 7 of Jordan & Gilbert (1920), just before *Thyrsocles*. Both names on that page are however not validly available, as they are just names, without indication, description or definition (*cf.* International Commission on Zoological Nomeclature, 1999). *Thyrsion* and *Thyrsocles* are mentioned for the second time on page 13 of Jordan & Gilbert (*l.c.*), *Thyrsion* before *Thyrsocles*, but again not as valid names. These names are mentioned for a third time on page 14 of Jordan & Gilbert (*l.c.*), with a short definition of each supposed taxon, which makes each name valid according to the ICZN (International Commission, 1999) and in this case also, *Thyrsion* is mentioned before *Thyrsocles*. This would surely give *Thyrsion* preference over *Thyrsocles*, as *Thyrsion* is validly published before *Thyrsion*. This is also the case for their full descriptions, *Thyrsion* on page 17 and *Thyrsocles* on page 19 (Jordan & Gilbert, 1920). Hence, it is clear that *Thyrsion* has preference over *Thyrsocles*.

Thyrsion is normally included with the Euzaphlegidae (see David, 1943, Danil'chenko, 1960). I believe however, that the Euzaphlegidae are a polyphyletic group and therefore invalid.Another member of the so-called Euzaphlegidae, *Palimphyes*, possesses gempylin apomorphies. The phylogenetic position of *Thyrsion* within scombroids is as of yet unclear. *Thyrsion* has always been associated with scombroids (see Jordan & Gilbert 1920, 1921; David, 1943). It possesses for example a non-protractile upper jaw. However, *Thyrsion* does not possess any synapomorphies for any known scombroid families, and no autapomorphies to stand as a monotypic subfamily on its own.

Thyrsion kriegeri (Jordan & Gilbert, 1919) comb. nov. (Fig. 7.75)

Thyrsites kriegeri Jordan & Gilbert, 1919: 41, Plate XVII, fig. 2. Type loc. Lompoc CA, U.S.A., Miocene.

Thyrsion velox Jordan in Jordan & Gilbert, 1920: 17, Plates VIII, IX. Type loc. *ibid.*

Thyrsocles kriegeri Jordan & Gilbert, 1920: 20, Plates XI, XII. Type loc. *ibid.*

Thyrsocles escharion Jordan in Jordan & Gilbert, 1920: 21. Type loc. *ibid.*

Thyrsocles velox Jordan, 1921: 274, Plate 6a. Type loc. *ibid.*

Referred material. USNM 10283 (Fig. 7.75a) and 11059 (Fig. 7.75b), Lompoc, California, U.S.A., Miocene Diatomaceous beds; USNM 10963, Late Miocene (Puente Formation).

Diagnosis. As for genus.

Description. The first descriptions of this species, under different guises, are given by Jordan (1921). and Jordan & Gilbert (1919, 1920) and do not present a coherent sythesis. For a good description of this species, based on many specimens, I refer to David (1943). Additional information and different observations are given here. It must be said here, though, that some meristic counts and other characters could not be drawn from the specimens that I studied. David recorded vertebral counts of 49-50 (-51). In specimens I have seen these counts are >43, 46 and >48 (see also *Remarks*). USNM 11059 (Fig. 7.75a) seems to have 19 precaudal vertebrae, although David states that there are 22-23 precaudal vertebrae. David counted 18 pectoral fin rays in specimens of *T. kriegeri*. In USNM 10963 (Fig. 7.75) I counted 17. The anal fin seems to be preceded by II spines.

Remarks. Jordan (1921) recognised two species "*Thyrsocles kriegeri*" and "*Thyrsocles velox*". David (1943) includes *Thyrsocles velox* in the synonymy of *Thyrsocles kriegeri*. I have here followed David, and recognised only one species *Thyrsion kriegeri*. Jordan (1921) does not manage to convince that there are really two species. He stated that *T. velox* differs from *T. kriegeri* in having shorter interhaemal bones (=anal pterygiophores). In comparing specimens labelled as

either *T. kriegeri* or *T. velox*, I failed to see a significant difference at that point. Another difference, supposedly, is that *T. velox* has a large mouth. However, a large mouth is a generic character of *Thyrsion* as a whole and Jordan's (1921, plate 36b) figure of *Thyrsocles kriegeri* shows a mouth that is certainly not smaller than that of "*T. velox*" ("...maxilla more than half head...", Jordan, 1921). *T. velox* is reported to have about 50 vertebrae and *T. kriegeri* 48. I have little confidence in these meristic counts as a dividing line. In the specimen labelled *T. kriegeri* (USNM 10283), 43 vertebrae are preserved. However, the specimen is damaged such that the accurate number of vertebrae is unknowable. Specimen USNM 11059 ("*T. velox*") has 46 vertebrae and USNM 10963 (also "*T. velox*"), with parts of the vertebral column missing, has 48 vertebrae preserved. Jordan (1921) suggested of *T. velox*: "It may be that this species is merely an extreme form of *T. kriegeri*". Based on previous descriptions and my study of these three specimens, I see no grounds in separating *Thyrsion* into different species. An exact vertebral count for this species is uncertain based on the specimens I have seen, but it seems to vary around 46. If there are sharp differences that would warrant a separation into two species, then these should be found in the holotypes, which I have not seen.

Genus ***Wetherellus*** Casier, 1966

Pachycephalus Agassiz, 1833-44: 139; Agassiz, 1845: 308 (*nomina nuda*).

Indeterminable, Woodward, 1901: 612.

Wetherellus Casier, 1966: 262, text-fig. 60-62, 73A, pl. 36, 37, figs. 1-3; pl. 38. Type loc. Sheppey, England, Eocene.

Diagnosis. Double tooth row, both rows seemigly cover whole length of tooth bearing bone. Differs from other genera with double tooth row (*Scombramphodon*, *Duplexdens*), which also have a deeply emarginated, fork-shaped ethmoid. In *Wetherellus*, the ethmoid is only slightly emarginated.

Type species. Only one species known, described below.

Species composition. Casier (1966) describe three species of *Wetherellus*, all from the Ypresian London Clay sediments. Bannikov (1985) expressed his suspicion that all three species of *Wetherellus*, as described by Casier (1966) are identical. My investigations provide evidence that Bannikov's suspicion was justified. Hence, one species *Wetherellus cristatus* Casier, 1966 is described below, along with the reasons for lumping the three previously known *Wetherellus* species into one.

Wetherellus cristatus Casier, 1966 (Fig. 7.76)

Pachycephalus cristatus Agassiz, 1833-44: 139; Agassiz, 1845: 308 (*nomina nuda*).

Indeterminable, Woodward, 1901: 612.

Wetherellus cristatus Casier, 1966: 263, text. fig. 60-62, 73A, pl. 36, pl. 37, figs. 2, 3. Type loc. Sheppey, England, Eocene.

Wetherellus brevior Casier, 1966: 270, pl. 38. Type loc. *ibid.*

Wetherellus longior Casier, 1966: 270, pl. 37, fig. 1. Type loc. *ibid.*

Diagnosis. As for genus.

Referred material. BMNH 269891 (**holotype** of *Wetherellus brevior*, Fig. 7.76a), 28498, (**holotype** of *Wetherellus cristatus*, Fig. 7.76b), P26719 (old P1698, **paratype** of *Wetherellus cristatus*), P45045 (old P1758a, **paratype** of *Wetherellus cristatus*), P45047 (old 30893, **holotype** of *Wetherellus longior*, Fig. 7.76c), P45048 (old 38093a, **paratype** of *Wetherellus cristatus*), Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. Species described in detail under three different names, which are mentioned above in synonymy. Casier's (1966) *W. cristatus* is described in more detail than the other two "species". Differences with Casier's descriptions and additional information are noted here. Supratemporal groove short, ending before middle of orbit. Postero-superior fossa also behind middle of orbit. Pterotic with short spine. Intercalar with short, inconspicuous posterior projection. Tooth rows double, teeth of inner and outer row almost of same size, inner teeth slightly larger. Ceratohyal with straight ventral margin. Hyoidean window present. Ethmoid slightly emarginated, but not fork-shaped as in Scomberomorinae, *Acanthocybium* and fossils such as *Scombramphodon*.

Remarks. I recognise here only one species, instead of the three different species erected by Casier (1966). Casier seems to treat the presence of a double tooth row in "*W. brevior*" as a special feature, one of those he uses to erect the species. The teeth are not well preserved in specimens of "*W. cristatus*" and "*W. brevior*". Hence, Casier was not justified in supposing that they had a single tooth row and that a multiplied tooth row was an apomorphy for "*W. brevior*". Casier (1966) based *W. longior* in part on that its exoccipital is longer than in other *Wetherellus*. Although the exoccipital might have been longer in *W. longior*, the difference does not seem significant in the studied specimens. Moreover, in "*W. cristatus*" and "*W. brevior*" specimens the exoccipitals cannot be properly investigated, because they are connected to the first vertebra, which obscures the image of the exoccipital. The exoccipital seems longer in "*W. longior*" because it is fully exposed. I have failed to see any significant differences between the different "species" of *Wetherellus*. I assume that they belong to the same species, which is characterised by a double tooth row.

Genus ***Woodwardella*** Casier, 1966

Woodwardella Casier, 1966: 289, text-fig. 67, pl. 25, fig. 3.

Diagnosis. Postero-superior fossae near anterior margin of orbit.
Type species. Only one species known, described below.
Species composition. Type species only.
Remarks. *Woodwardella* is probably a scombrid. it shares a vomerine character with scomberomorinae and *Acanthocybium* (see below). However, in the provisional cladogram of scombroids (Chapter 8) its place within the scombroids is unresolved.

Woodwardella patellifrons Casier, 1966 (Fig. 7.77)

Woodwardella patellifrons Casier, 1966: 290, text-fig. 67, pl. 25, fig. 3. Sheppey, England, Eocene.

Diagnosis. As for genus.
Referred material. BMNH P26903 **(holotype)**, Sheppey, England, Early Eocene: Ypresian (London Clay).
Description. A description is given by Casier (1966). Additional information and differences are given here. Premaxilla forms non-protrusible complex with maxilla. Supratemporal groove relatively short, reaching up to anterior margin of orbit, which is also location of muscle attachments (postero-superior fossa). Because of damage in specimen not clear if pineal window present or absent. Pterotic spine short, reaching up to base of exoccipital. Anterior margin of vomer spatulate, as in scomberomorinae and *Acanthocybium*. Ceratohyal without ventral projections or ceratohyal window. Scales on opercular bones large.

Suborder ***INCERTAE SEDIS***

Genus ***Aglyptorhynchus*** Casier, 1966

Cylindracanthus Leriche, 1908: 381.

Glyptorhynchus Leriche, 1910: 339, figs. 137-144, pl. XXV, figs. 3-6 (*pro parte non* Leriche, 1906).

Aglyptorhynchus Casier, 1966: 303.

Diagnosis. Known from rostra only (Fig. 7.78a). Cross-section at base of "rostrum" almost square (Fig. 7.78b), and circular near anterior tip (Fig. 7.78c). Four nutrient canals which at base of "rostrum" occupy almost the whole of the area in transverse cross-section (compare Figs. 7.78b, c).

Type species. Aglyptorhynchus denticulatus (Leriche, 1908).
Species composition. Eleven species are recorded in Schultz (1987), from the Early Eocene to Late Oligocene. I have studied a few specimens of *Aglyptorhynchus venablesi* Casier, 1966.
Remarks. Leriche (1906) realised that the name *Coelorhynchus* for fossil billfish rostra was preoccupied by a Recent marcurid. He thus introduced the new generic name *Glyptorhynchus*, apparently unaware of an already existing valid generic name *Cylindracanthus* Leidy, 1856. Leriche (1908, 1910) subsequently regards *Glyptorhynchus* as a subgenus of *Cylindracanthus*. However, the *Glyptorhynchus* Leriche (1906) described concerns what is now known as *Cylindracanthus* (see below) and the *Glyptorhynchus* described by Leriche (1910) is generically different from *Cylindracanthus*. Casier (1966) erected the new genus *Aglyptorhynchus* for the taxa that fit Leriche's (1910) diagnosis of *Cylindracanthus* subgen. *Glyptorhyncus*.

This genus is represented by fossils of rostra only. Judging by its four nutrient canals and multiple tooth rows (Fig. 7.78d), it is likely that *Aglyptorhynchus* is a billfish, maybe related to *Xiphiorhynchus*. If it is a billfish rostrum, it is morphologically distant from any billfish, also from *Xiphiorhynchus*. In shape and size it also resembles a long spine, which was, at one side, covered by denticles rather than premaxillary teeth. Additional material is needed than rostra alone to confirm whether *Aglyptorhynchus* is indeed a billfish. For the phylogenetic analysis, *Aglyptorhynchus* contains just two characters (rostrum present, multiple tooth rows) which are neither unique nor in a unique combination. There are no characters which confirm a relationship to scombroids. Hence, *Aglyptorhynchus* is excluded form the phylogenetic analysis.

Aglyptorhynchus venablesi Casier, 1966 (Fig. 7.78)

Aglyptorhynchus venablesi Casier, 1966: 305, text-fig. 71, pl. 51, figs. 1-3, Pl 61. Type loc. Bognor Regis, England, Eocene.

Diagnosis. As for genus. No other *Aglyptorhynchus* species studied.
Referred material. BMNH P27612-4 (**paratypes,** Fig. 7.78b) and P27615 (**holotype,** Figs. 7.78a, c, d), Bognor Regis, Sussex, England, Ypresian (Fish tooth bed of London Clay).
Description. See Casier (1966).

Genus *Ardiodus* White, 1931

Ardioudus White, 1931: 89. Plate figs. 4-5.

?*Ardiodus* Casier, 1966: 297.

Diagnosis. Known from teeth only. Unique combination of characters. Teeth resemble subconical, short, stout teeth of Scomberomorinae, but *Ardiodus* teeth more curved. Similarity between *Ardiodus* and *Eocoelopoma* remarked (Casier, 1966 and pers. obs.). However, *Ardiodus* teeth larger than those of *Eocoelopoma*. Largest *Ardiodus* tooth seen with crown of 8 mm. Largest *Eocoelopoma gigas* teeth 6 mm long. Furthermore, *Eocoelopoma* teeth without lateral cutting edge as seen in *Ardiodus*. Although shorter and stouter than gempylin or trichiurin teeth, barbed apex, as found in *Ardiodus*, also occurs in gempylins and trichiurins.

Type species. *Ardiodus mariotti* White, 1931 (England, Late Palaeocene: Oldhaven Beds-Early Eocene: Ypresian and Morocco, Late Palaeocene-Early Eocene: Thanethian-Ypresian).

Species composition. Only the type species.

Remarks. Although known of teeth only, as *Ardiodus* is most likely to be a scombroid. There are resemblances to gempylins, trichiurins, *Eocoelopoma* and Scomberomorinae. Casier (1966) also remarks resemblances to *Eutrichiurides* and *Scombramphodon* Woodward (1901) and Danil'chenko (1960) place *Ardiodus* in the Trichiurinae, most likely because of the barbed teeth. I do not recognise this as an apomorphy exclusive to the trichiurins. Although the teeth show an interesting combination of characters, there are not enough to include *Ardiodus* in the phylogenetic analysis. Until associated bones are found with teeth, the identity of *Ardiodus* will remain somewhat mysterious.

Ardiodus mariotti White, 1931 (Fig. 7.79)

Ardiodus mariotti White, 1931: 89, Plate figs. 4-5. Type loc. Upnor, England, Palaeocene.

?*Ardiodus mariotti* Casier, 1966: 297.

Diagnosis As for genus.

Referred material. BMNH P14809 (Fig. 7.79), Upnor, Kent, England, Late Palaeocene (Oldhaven Beds); P26601-4, Sheppey, Early Eocene: Ypresian (London Clay); P42689, Bognor Regis, Sussex, England, Early Eocene: Ypresian (Lower Fish-tooth Bed, London Clay), P38281-3, Morocco, Late Palaeocene-Early Eocene: Thanetian-Ypresian (Phosphates).

Description. Base of tooth circular (especially in the larger specimens) to semicircular. Crown becoming more labio-lingually compressed towards apex. Two lateral non-serrated cutting edges present. Apical barbs in most teeth. Largest tooth 8 mm (in sample BMNH P14809). Striations on surface of tooth variable:

seemingly smooth (but under binoculars, faint striations visible), basally straited to completely and densely striated.

Remarks. The spatial distribution of this species is somewhat suspect. The only specimens known so far are found in England and Morocco. This is the first report of Moroccan *Ardiodus*. Also, all Moroccan teeth seem smooth at first sight, although faint striations are visible under binoculars. The English teeth show a large variety, from hardly to densely striated. This might suggest that the Moroccan fossils represent a different variety or even a different species. However, the degree of striations of the Moroccan sample does fit in with the variety as seen in the English specimens and there seem to be no other diagnostic characters. Hence, the Moroccan samples are also identified as *A. mariotti*.

Unknown

cf. Planesox vorax Woodward, 1901: 519.

Indeterminable percomorph, Casier, 1966: 317.

Referred material: BMNH P26709 (skull), Sheppey, England, Early Eocene: Ypresian (London Clay). Labelled as "*Planesox vorax*'.

Description/Remarks. Woodward (1901) mentioned this specimen, using the older collection number P1998x as an unidentifiable percid. Woodward considered the specimen in question to be similar to *Planesox vorax*, as he did with what later became the holotype of *Progempylus edwardsi* (see Casier, 1966). The name *Plaesox* cannot be assigned to this specimen, not only because Owen's "type" is missing, but also because it cannot be verified if this specimen has an edentulous maxilla, which is characteristic for Owen's *Planesox* (Owen, 1854). Viewed from dorsal, the cranium of P26709 does resmble a gempylin one but it lacks any clear generic and specific apomorphies. Only a few generalised comparisons with other taxa can be made. The operculum of this specimen seems much larger than in known gempylins. The skull as a whole is also shorter than expected from a Gempylinae. Viewed from lateral, it reminds more of a skull belonging to a Sardini of Thunnini. However, the cranium is clearly elevated, as opposed to the flat cranium of tunas and bonitos. Furthermore, the absence of the premaxillary-maxilla complex makes it unsure wheter this specimen belongs to the scombroids at all.

Incertae sedis non Xiphiinae

The taxa described in this section concern those that have been described as belonging to the billfishes. In my investigation of the fossil material in question I

found no strong evidence to support assignment to billfish. I am particularly concerned about "billfish rostra" based taxa such as *Cylindracanthus* (see below), of which I am uncertain if these do concern teleosts or even fish at all.

Genus *Acestrus* Woodward, 1901

Acestrus Agassiz, 1845: 308 (*nomen nudum*).

Acestrus Woodward, 1901: 494, pl. XIX, fig. 3.

Diagnosis. Postero-superior fossae placed posterior of orbit.

Type species. *Acestrus ornatus* Woodward, 1901.

Species composition. Only the type species. *Acestrus elongatus* Casier, 1966 is not recognised here. Its holotype, BMNH P12954, bears only a superficial resemblance to *Acestrus*, has longer supratemporal grooves and more anteriorly placed postero-superior fossae. Casier (1966) remarked similarities to *Scombrinus* (my *Duplexdens*). The specimen is here used as material to describe *Duplexdens* (see above).

Remarks. This genus is known by its braincase only. It was considered a scombroid because of similarities with *Xiphias* (Casier, 1966). However, these similarities come down to superficial resemblances, such as the shape of the cranium and the pattern of ridges on the skull roof. I have found no synapomorphies that validate the inclusion of *Acestrus* in Scombroidei. The upper jaw is missing, so it is not known whether the maxilla and premaxilla formed a non-protrusible complex. It is also not known whether *Acestrus* possessed a rostrum as in billfishes, so affinities to *Xiphias* cannot be assessed. The identity and affinities of *Acestrus* remain a mystery for now. This genus is not included in the phylogenetic analysis, due to a lack of characters and apomorphies.

Acestrus ornatus Woodward, 1901 (Fig. 7.80)

Acestrus ornatus Agassiz, 1845: 308 (*nomem nudum*).

Acetrus ornatus Woodward, 1901: 494, pl. XIX, fig. 3. Type loc. England, Eocene.

Diagnosis. As for genus.

Referred material. BMNH 627 (**holotype,** Fig. 7.80a), P1793, P60905 (Fig. 7.80b), Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. Descriptions are given by Woodward (1901) and Casier (1966).

Genus *Cylindracanthus* Leidy, 1856

Coelorhynchus Agassiz, 1833-44: 92; Williamson, 1849: 471 (*nomina nuda, non* Giorna, 1805).

Coelorhynchus Dixon, 1850: 112, pl. 10, figs. 14-17; pl. 11, fig. 26.

Cylindracanthus Leidy, 1856: 12.

Diagnosis. "Rostra" with almost circular cross-section, whole outer surface with parallel lengthwise grooves, two large and two small nutrient canals (sometimes the small canals are missing) and two narrow, widely separated tooth rows.

Type species. Cylindracanthus rectus (Dixon, 1850)

Species composition. Six species are known, known to occur from the Cenomanian (Late Cretaceuous) to the Priabonian (Late Eocene), but possibly occurring in the Pliocene (Schultz, 1987). I have studied specimens of *C. rectus* and *Cylindracanthus gigas* (Woodward, 1888). One specimen (BMNH P48574) from the Late Cretaceous of Syria could not be specifically identified.

Remarks. Cylindracanthus remains are often diagnosed as billfish because they superficially remind of rostra, and possess what are interpreted as nutrient canals. However, I feel that these fossils differ too much from any known Recent or fossil billfish. There are lengthwise grooves over the whole of the surface. This character state comes the closest to that in *Blochius*, which appears to have lengthwise grooves in the dorsal surface of thhe rostrum but not in the ventral surface. *Cylindracathus* is also much more conical throughout. In all billfishes there is a degree of flattening near the anterior tip of the bill, while in *Cylindracanthus* this flattening is absent. It has been suggested that the *Cylindracanthus* rostrum is a chimaeroid spine (see Woodward, 1891a). The bulk of the scombroid fossils appear in the Ypresian (Early Eocene). *Blochius*, by some thought to be related to *Cylindracanthus* (Casier, 1966; Schultz, 1987) does not appear in the fossil record before the Lutetian (Middle Eocene). If the basic groups of scombroids radiate about simultaneously, and much later than *Cylindracanthus*, it seems unlikely to me that the latter is a scombroid.

Cylindracanthus gigas (Woodward, 1888) (Fig. 7.81)

Coelorhynchus gigas Woodward, 1888: 225. Type loc. Great Sphinx, Egypt, Eocene.

Cylindracanthus gigas Weiler, 1929: 18. Type loc. *ibid.*

Diagnosis. Larger than other species. Maximum diameter about 17.8 mm. *C. rectus* has diameters between 7 and 11 mm.

Referred material. BMNH 893-5 (**holotype,** Fig. 7.81), rock of the Great Sphinx, Egypt, Eocene.

Description. Large and damaged spine-like structure, about 17.8 mm in diameter, with numerous narrow lengthwise grooves. Transverse cross-section circular.

Cylindracanthus rectus (Dixon, 1850) (Fig. 7.82)

Coelorhynchus rectus Agassiz, 1833-44: 92 (*nomen nudum*). Type loc. ?Bracklesham Bay, England, Eocene.

Coelorhynchus rectus Dixon, 1850: 112, pl. 10, figs. 14-17; pl. 11, fig. 26. Type loc. *ibid.*

Cylindracanthus ornatus Leidy, 1856: 12. Type loc. ?

Coelorhynchus burtini Le Hon, 1871: 14. Type loc.: Belgium, Eocene.

Cylindracanthus rectus Leriche, 1910: 223 (*nomen nudum*).

Cylindracanthus rectus Leriche, 1920: 82. Type loc.: Congo-Kinshasa.

Diagnosis. Small compared to *C. gigas*: maximum diameter between 7 and 11 mm.

Referred material. BMNH 25859 (supposed **Syntype**), Bracklesham Bay, Sussex, England, Ypresian-Lutetian (Bracklesham Beds); 38881, Sheppey, England, Early Eocene: Ypresian (London Clay); 38881a, (Fig. 7.82.a) Sheppey, England, Early Eocene: Ypresian (London Clay); P4304 (Fig. 7.82b), Barton Cliff, Hampshire, England, Bartonian (Barton Clay); P6232, Sheppey, England, Early Eocene: Ypresian (London Clay); P11845-8, Ameki, Ombialla District, Nigeria, Lutetian.

Description. Long and slender spine-like structure, 7-11 mm in diameter, with numerous narrow lengthwise grooves. Transverse cross-section circular. In ventral grooves immediately next to midline of BMNH 38881 are badly preserved empty tooth sockets. These grooves are about 1 mm wide. In some specimens, there are two pairs of "nutrient canals", a pair of larger and a pair of smaller canals (Fig. 7.82a). The large canals diminsh in size anteriorly. There are also specimens that have one pair of large canals that coalesce into a single large canal anteriorly.

Remarks. Apart from disagreeing with the inclusion of *Cylindracanthus* as a billfish, I suspect that all the material described as *C. rectus* is heterogenous. The different system of "nutrient canals" as described above are rather different. I cannot believe that these specimens belong to the same specis, probably not to the same genus either. It is impossible to verify what the original *C. rectus* is like, since there is uncertainty towards which specimens were the original types. Thus, *C. rectus* should be typified as an indication for different kinds of spines whose origins are uncertain.

White (1926) described vertebrae which he supposed to be *Cylindracanthus rectus*. I described these vertebrae earlier on as Xipniinae indet.

Genus *Enniskillenus* Casier, 1966

Ptychocephalus Agassiz, 1833-44: 139 (*nnomen nudum*).

Ptychocepalus Agassiz, 1845: 307 (*nomen nudum*).

Palaeorhynchus? Woodward, 1901: 497.

Enniskillenus Casier, 1966: 299, text-fig. 70, pl. 54.

Diagnosis. Frontals dorsally convex (Fig. 7.83a) and provided with numerous minute perforations, postero-superior fossa placed posterior of orbit.
Type species. One species known, described below.
Species composition. Only the type species.
Remarks. Because of superficial resemblances, Casier (1966) concluded that *Enniskellinus* is a palaeorynchid. His reasons are: the postorbital part of the skull resembles that of Acanthopterygii, the skull is elongated, and the orbits are large (Fig. 7.83b). However, the skulls do not reveal any synapomorphies for palaeorhynchins, billfishes, or even scombroids. The jaw apparatus is missing, as is the whole of the postcranial skeleton. The apomorphies of the frontals (see above) are not seen in any bliffish. I find it impossible at this point to assess the phylogenetic position of this genus and I excluded it from the cladistic analysis.

Enniskillenus radiatus Casier, 1966 (Fig. 7.83)

Ptychocephalus radiatus Agassiz, 1833-44: 139 (*nnomen nudum*).

Ptychocepalus radiatus Agassiz, 1845: 307 (*nomen nudum*).

Palaeorhynchus? Woodward, 1901: 497.

Enniskillenus radiatus Casier, 1966: 299, text-fig. 70, pl. 54. Type loc. Sheppey, England, Eocene.

Diagnosis. As for genus.
Referred material. BMNH 33136 (**paratype**), P646 (**holotype,** Fig. 7.83), P1741 (**paratype**) and P26893 (**paratype**), Sheppey, England, Early Eocene: Ypresian (London Clay).
Description. A detailed description is given by Casier (1966).

Genus *Hemirhabdorhynchus* Casier, 1946

Glyptorhynchus Leriche, 1926: 121-124 (*pro parte non* Leriche, 1906).

Hemirhabdorhynchus Casier, 1946: 155.

Diagnosis. Small "rostrum" with four large dorsal crests, two widely separated tooth rows, two large and two small nutrient canals.
Type species. Hemrhabdorhynchus costatus (Leriche, 1926).
Species composition. Five species are known (Schultz, 1987 omitted *Hemirhabdorhynchus elliotti* Casier, 1966 from his species list without any known

reason), found between Early and Middle Eocene sediments. I have studied the only known specimen of *H. elliotti.*

Remarks. Hemirhabdorhynchus has long been considered a billfish or a "blochiid" (Casier, 1946 and 1966; Schultz, 1987). However, the morphology and the size of the *Hemirhabdorhynchus* "rostra" reveal only little agreement with any known billfish. The shape in cross-section, large crests and the two separate narrow tooth rows are very unusual for billfish. Since *Hemirhabdorhynchus* is only known from these "rostra" I have no confidence in their recognition as billfish remains. There are no synapomorphies with billfishes or even scombroids. Rather than rostra, *Hemirhabdorhynchus* resembles more a hollow spine with two rows of denticles. I thus consider the systematic status of this taxon unknown.

Hemirhabdorhynchus elliotti Casier, 1966 (Fig. 7.84)

Hemirhabdorhynchus elliotti Casier, 1966: 175, text-fig. 30, pl. 22, fig. 6. Type loc. Sheppey, England, Eocene.

Diagnosis. As for genus. No other species studied.

Referred material BMNH P21304 (**holotype,** Fig. 7.84), Sheppey, England, Early Eocene: Ypresian (London Clay).

Description. Description given by Casier (1966). In that description, two large nutrient canals are mentioned, while I believe there is a pair of dorsal small canals as well (Fig. 7.84a).

CHAPTER 8: PHYLOGENETIC ANALYSES

8.1 Material and methods

All the cladistic analyses described below were carried out on a computer operated by MacOS 9.04 with a 300 MHz G3 processor. The data matrix has been subjected to several tests. First, tests using PAUP* (Swofford, 2000) were carried out, in which *Sphyraena* was included as an outgroup taxon, along with the taxa indicated as outgroup taxa in Table 1.1. This was considered the "blank hypothesis", that served as a reference point for tests to determine the definite borders of ingroup and outgroup taxa in the final analysis. The following hypotheses were tested: 1. Is *Sphyraena* an ingroup or an outgroup taxon, possibly related to mugilids? 2. Is *Gasterochisma* an aberrant scombrid, or an unusual percoid? 3. Are billfishes part of the Scombroidei or an outgroup taxon, maybe related to *Corphyaena*? The different hypotheses are tested by generating different trees, using enforced topological constraints. The measure to test each hypothesis is that of parsimony. In each test, the length of the tree, with for example the forced constraint that sphyraenids belong to the outgroup, is compared to the blank test tree. Six tests were performed, in which the composition of ingroup and outgroup varied: 1: *Sphyraena*, *Gasterochisma* and billfishes included in the ingroup, 2: *Sphyraena* in outgroup, *Gasterochisma* and billfishes in ingroup, 3: *Sphyraena* and *Gasterochisma* in outgroup, billfishes in ingroup, 4: *Sphyraena* and billfishes in ingroup, *Gasterochisma* in outgroup, 5: *Sphyraena* in ingroup, billfishes and *Gasterochisma* in outgroup, 6: *Sphyraena* and *Gasterochisma* in ingroup, billfishes in outgroup.

All characters were treated as unordered, even if a transition series was known. If there is a fixed evolutionary sequence, it will come out right in the distribution of character states on the cladogram. If there is no fixed evolutionary pathway, this will also be reflected in the distribution of character states. Thus, treating all characters as unordered removes some *a priori* bias, will reproduce an objective result, be the evolution ordered or unordered; and is less labour-intensive for the phylogenetic analyst.

8.2 Generation of blank test tree

First, the minimal length trees expressing the "blank hypothesis" was determined. The blank hypothesis is that where apart from the outgroup taxa in Table 1.1, *Sphyraena* is also included in the outgroup. The length of this tree was determined by enforcing the topological constraint that taxa 5 to 75 of the data matrix form a monophyletic group. At this point, the topology of the test tree was

not relevant, only its length. An efficient way to discover the minimum tree length is by, in PAUP*, turning the MULTREES option off, so that if multiple trees of the same length exist, only one is saved. This prevents computer memory being overflowed by numerous trees, while being guaranteed to find the shortest tree length. However, the total population of trees to swap on is drastically decreased with the MULTREES option off. This increases the possibility that the samples taken by heuristic searches are not representative for the population, and that optimal trees are not found. This is where the trial-and-error nature of heuristic searches (Kitching *et al.*, 1998) could be at its weakest. This problem can be tackled by significantly increasing the number of random addition sequences. The default is 10 replicates, but in this test I let PAUP* perform 2,000 random addition sequence replicates. Performing the search with a large number of replicates not only increases the probability of finding optimal trees, but still performs the search within an acceptable time (approximately 1 hour and 50 minutes if run in foreground). Before the matrix was treated by PAUP* according to the above described method, safe character taxonomic deletion was performed to enhance the performance of PAUP* and yet retain the maximum information possible in resulting cladograms.

There are only two uninformative characters s uncovered by PAUP*: character 40 (presence or absence of mid-lateral dent in vertebrae) and 45 (presence or absence of bullae on vertebrae 5-12).

A method of safe taxa deletion was brought forward by Wilkinson (1995). A computer program (TAXEQ2, of Wilkinson, 1995b) was written to provide tools for such safe taxonomic deletion. Analysis of the data matrix with TAXEQ2 showed that there are five OTUs without unique combinations of character states: *Casierichthys*, *Eutrichiurides*, ?Gempylinae indet., *Stereodus* and Thunnidae indet. It is mentioned in § 7.3 that the systematic status of *Eutrichiurides* is not clear due to lack of apomorphies. Also, the ?Gempylinae indet. is a skull, seemingly without clear apomorphies, but due to superficial resemblances is probably a gempylin, possibly a trichiurin. Thus, it is not surprising that these OTUs are shown not have unique (combinations of) character states by the TAXEQ2 algorithm. I also decided to delete one more taxon, although the TAXEQ2 output did not classify it as safely deletable. I believe that *Palaeocybium* and *Acanthocybium* are closely related, based on dental characters. A synapomorphy for a clade containing both would be that their teeth are more laterally compressed, blunt-tipped and tightly packed than in other taxa (character 22, state 1). In *Acanthocybium* this condition is further derived, because its teeth are also serrated (character 22, state 2). From this point of view, *Palaeocybium* appears to be more primitive than *Acanthocybium*. Another synapomorphy for *Acanthocybium* and *Palaeocybium* would be the mid-lateral dent in the vertebrae (character 40) However, character 40 is always indicated

as parsimony uninformative by PAUP*. In view of this and the many missing entries of *Palaeocybium* (74) it was decided to also eliminate *Palaeocybium* from the analysis. *Palaeocybium* does not seem to have any other characters preserved that provide information on relationships with other taxa, or on relationships of an *Acanthocybium+Palaeocybium* clade to other taxa.

The "reduced" data matrix now, without the taxa to be deleted and the uninformative characters 22, 40 and 45 removed, was executed in PAUP*. The characters were not weighed. In the matrix, polymorphic character states are indicated between round brackets and uncertain multistate entries in accolades. The chosen optimisation criterion was DELTRAN. Two thousand random addition sequences were performed with TBR swapping on the best starting trees, Steepest descent turned on and MULTREES off. An analysis, carried out as described above, resulted in 17 shortest trees of the "blank hypothesis" of 386 steps.

8.3 Ingroup/outgroup tests

I have carried out several tests to determine which is the most parsimonious composition of ingroup and outgroup. Tree searches were performed in PAUP*, according to the same methodology with which the blank test hypothesis tree length was determined (see above). Of the three taxa whose ingroup/outgroup position is not clear, *Sphyraena*, *Gasterochisma* and billfishes, all combinations of respective in- or outgroup positions were determined (see Table 8.1). The length of each hypothesis was determined by searching for tree lengths, enforcing the topology of a monophyletic ingroup that agrees with the outgroup as represented in the hypothesis to test. The results of these tests, in Table 8.1 indicate that there is not one single most parsimonious

Table 8.1. Shortest tree lengths of various ingroup (IN)/outgroup (OUT) hypotheses. *Gasterochisma* included.

Tested hypothesis	Tree length (steps)
Sphyraena: OUT, *Gasterochisma*: IN, billfishes: IN (blank)	386
Sphyraena: OUT, *Gasterochisma*: OUT, billfishes: IN	386
Sphyraena: OUT, *Gasterochisma*: IN, billfishes: OUT	385
Sphyraena: OUT, *Gasterochisma*: OUT, billfishes: OUT	385
Sphyraena: IN, *Gasterochisma*: IN, billfishes: IN	385
Sphyraena: IN, *Gasterochisma*: OUT, billfishes: IN	387
Sphyraena: IN, *Gasterochisma*: IN, billfishes: OUT	386
Sphyraena: IN, *Gasterochisma*: OUT, billfishes: OUT	386

solution. Based on the data presented in Table 8.1, *Gasterochisma* seems to be a problematic taxon. When the billfishes are moved from ingroup to outgroup or from outgroup to ingroup, the tree length changes. The same holds for movements of *Sphyraena*. When *Gasterochisma* is moved, however, it influences the tree length on only one occasion: when both *Sphyraena* and billfishes are in the ingroup. I suspect that the presence of *Sphyraena* in the data matrix sends many conflicting signals. *Gasterochisma* possesses a remarkable combination of primitive and advanced characteristics (see also Chapter 1). I think that, because *Gasterochisma* sends conflicting signals, there is no single most parsimonious ingroup/outgroup hypothesis amongst those in Table 8.1. Further ingroup/outgroup tests were done, according to the same methodology as described § 8.2, but then without *Gasterochisma*. The results (Table 8.2) are significantly different. Not only are the trees 12-15 steps shorter than those in Table 8.1, there is one most parsimonious solution: *Sphyraena* in the outgroup; billfishes in the ingroup. Hence, I decided to continue with the cladistic analysis without *Gasterochisma*, keep *Sphyraena* in the outgroup and billfishes in the ingroup.

Table 8.2. Tree lengths of various ingroup (IN)/outgroup (OUT) hypotheses. *Gasterochisma* deleted.

Tested hypothesis	Tree length (steps)
Sphyraena: OUT, billfishes: IN (blank)	372
Sphyraena: OUT, billfishes: OUT	373
Sphyraena: IN, billfishes: IN	373

8.4 A cladistic hypothesis for scombroids

The result of the search for the shortest tree length, with 2,000 random addition sequence replicates and MULTREES off, resulted in five trees of 372 steps. The next step was to find all, or a representative sample, of the possible trees of 372 steps. To achieve this, a search with 2,000 random addition sequence replicates was started, with the option MULTREES on and saving no more than one tree of ≥373 steps during branch swapping. However, in doing so, PAUP*'s memory became overloaded with trees of 372 steps. With more than 60,000 trees in memory, branch swapping progressed very slowly (close to "freezing point"), and if there was visible progress, the number of trees left to swap increased. I felt that the computer did not have the memory to adequately deal with the search and was not sure if there was a representative sample of parsimonious trees in memory, hence the heuristic search was aborted. In the hope of retrieving that representative sample, I decided to yet again turn off the MULTREES option and increase the

number of addition sequence replicates to 5,000. This resulted in twelve trees of 372 steps. Although I do not feel certain that so low a number of most parsimonious trees is representative for the total population of most parsimonious trees (with MULTREES of I would probably obtain many more than 60,000 in total), I decided to continue with these twelve trees to postulate a (provisional) phylogenetic hypothesis for scombroids. Of these five trees, five consensus trees were constructed: a strict, combinable components, 50% majority rule, Adams and strict reduced tree. The strict consensus tree showed little resolution, but I was surprised to see that it was not much better in the combinable components ("semistrict") consensus tree or the strict reduced consensus tree. The strict reduced consensus tree was constructed using the program RadCon (Thorley & Page, 2000). The best resolution was contained in the Adams consensus tree (Fig. 8.1). Bootstrap values were obtained by performing 180 bootstrap replicates. Each bootstrap replicate consisted of resampling heuristic searches, in each of which 200 random addition sequence replicates were carried out, with the MULTREES option turned off. Decay indices (Bremer support values) were calculated using the program AutoDecay (Eriksson & Wikström, 1996), that writes a batch PAUP command file. The PAUP* output of that file was used to calculate the decay indices. A cladogram without the fossil taxa was also produced, according to the same methodologies as the tree with fossils (5,000 heuristic replicates with MULTREES off and a topological constraint, which implies *Sphyraena* in outgroup and billfishes in ingroup, enforced). this tree is pictured in Fig. 8.2.

The construction of a cladogram using this matrix proved to be problematic. The Adams consensus cladogram presented in § 8.4 is included here only as a provisional hypothesis and should not be taken as a definite solution. The data matrix, as presented here, gives rise to a vast number of (sub)optimal trees, which means that "severe" measures, such as turning MULTREES off, saving trees of only certain lengths and enforcing constraints have to be used to obtain results with which one can work. The Adams consensus is used to obtain enough resolution in the phylogenetic hypothesis, because other consensus methods, which I feel would be preferable on theoretical grounds, did not provide enough resolution. The indices of every individual tree on which the consensus is based are as follows. Consistency index (CI): 0.376, Retention index (RI): 0.759 . The bootstrap supports are alarmingly low. Part of that may have been my methodology to obtain these values, but I felt any other way would overflow the memory. The only reason that the Scombroidei node is supported by 100% bootstrap replicates, is because of enforcement of a topological constraint, besides that, there is no single node with strong enough support (≥95%). The decay indices reveal something more: the fact that they are all negative, indicates that this is not the shortest tree to be found. Within the time framework, however I felt that I had no opportunity left to review

the data on which the tree is based. I feel have made the best possible consensus between search accuracy and time available. I would like to stress again at this point, that this is not a definite hypothesis. Character state changes were made visible by mapping them onto the tree, using the computer program MacClade (Maddison & Maddison, 1997). Many cases of independent acquisitions and reversals can be seen. Many times, the character evolution on the tree showed a pattern differing from the one I expected. In some cases, there seemed to be no clear direction in the evolution of the character in question. I suspect that the root of my problems with obtaining a representative sample of most parsimonious trees lies here. There is an urgent need for re-interpretation of (some of the) used characters, and probably some characters should be deleted from the analysis, even though PAUP* deemed them to be parsimony-informative. I plan to proceed with this in the near future, and hopefully I can then produce a more robust (consensus) cladogram.

8.5 Implications of the provisional phylogenetic hypothesis

8.5.1 Phylogenetic implications

The phylogenetic hypothesis, as presented here, is to be seen as provisional, and should not be seen as a solution to the systematic problems of scombroids. However, the hypothesis drawn out here shows an interesting grouping of certain clades, which are worth noting and discussing. Probably most, if not some, of the relationships represented in the tree will also be present in a cladogram based on better interpretation of the characters, something that I hope to produce in the near future. Based on the topology of the cladogram and comparison with the cladogram without fossils, I propose the following (provisional) taxonomic division, made using the phyletic sequencing convention:

Suborder **Scombroidei**

Family **Trichiuridae**

Subfamily **Gempylinae:** *Thyrsites*, *Neoepinnula*, *Thyrsitops*, *Tongaichthys*, *Lepidocybium*, *Ruvettus*, *Rexichthys*, *Thyrsitoides*, *Nesiarchus*, *Nealotus*, *Dicrotus*, *Rexea*, *Gempylus*, *Diplospinus*, *Paradiplospinus*

cf. Subfamily **Gempylinae:** *Progempylus*, *Palimphyes*, *Abadzekhia.*

Subfamily **Trichiurinae:** *Anenchelum*, *Aphanopus*, *Assurger*, *Benthodesmus*, *Lepidopus*, *Eupleurogrammus*, *Trichiurus*, *Lepturacanthus*, *Tentoriceps*, *Evoxymetopon*, *Casierichthys.*

Family **Scombridae**

Subfamily **Scombrinae *sensu novo***: *Scomber*, *Rastrelliger*.

cf. Subfamily **Scombrinae**: *Scombrinus*.

Subfamily **Godsillinae subfam. nov.**: *Godsilla*.

Subfamily **Palaeothunninae subfam. nov.**: *Palaeothunnus*.

Subfamily **Scomberomorinae**: *Scomberomorus*, *Grammatorcynus*.

Subfamily **Sardinae subfam. nov.**

Tribe **Sardini**: *Gymnosarda*, *Stereodus*, *Cybiosarda*, *Sarda*, *Orcynopsis*.

Tribe **Thunnini**: *Allothunnus*, *Thunnus*, *Katsuwonus*, *Euthynnus*, *Auxis*.

Subfamily **Acanthocybiinae**: *Acanthocybium*, *Neocybium*, *Palaeocybium*, *Scomberodon*, *Gigantothazard*.

Subfamily **Eothynninae subfam. nov.**: *Eothynnus*

Subfamily **Xiphiinae**

Tribe **Xiphiorhynchini** *Xiphiorhynchus*, *Rotundorhynchus*

Tribe **Xiphiini**: *Blochius*, *Xiphias*.

Tribe **Istiophorini**: *Makaira*, *Tetrapturus*, *Istiophorus*.

Tribe **Palaeorhynchini**: *Makairoides*, *Homorhynchus*, *Palaeorhynchus*, *Pseudotetrapturus*.

Tribe ***incertae sedis***: *Rotundorhynchus*

Subfamily ***incertae sedis***: *Tamesichthys*, *Eocoelopoma*.

Family ***incertae sedis***: *Duplexdens*, *Microrhynchus*, *Scombramphodon*, *Sphyraenodus*, *Thyrsion*, *Wetherellus*, *Woodwardella*, gen. and spec. nov.

Some general implications of this taxonomic division are discussed below.

Outgroup/Scombroids. From the cladogram without fossils, the exact borders of the Scombroidei are not clear. If, according to that cladogram, the billfishes are scombroids, then they are only distantly related to the others. I however decided to follow the cladogram including fossils, in which the billfishes are part of the scombrids (see also below). According to the tests described above, it is more parsimonious for *Sphyraena* to be an outgroup- rather than an ingroup taxon. De Sylva (1984) considers *Sphyraena* to be closely related to the mugilids. Johnson (1986) considered *Sphyraena* as the most primitive scombroid. The cytochrome-*b* gene of *Sphyraena* proved not to be closely related to that of scombroids (Finnerty & Block, 1995). The topology of the cladogram with fossils does not make it clear whether *Sphyraena* and *Scombrolabrax* are outgroup taxa or primitive scombroids, but they are part of the specified outgroup used for rooting the tree. In the cladogram without fossils both are clearly in the outgroup, forming a monophyletic clade. Whereas Johnson (1986) found that *Sphyraena* shared his scombroid

synapomorphies, *Sphyraena* is apparently missing the synapomorphies here assigned to scombroids (see § 8.5.1.1). It is remarkable, though, that *Sphyraena* and mugilids are not closely related, even though both share remarkable apomorphies such as elongated and fimbriated epiotics and the possession of pseudo-predorsals. This is because the mugilids lack some key apomorphies which *Sphyraena* shares with other outgroup taxa, namely: character 10 (size of intercalary projection, in the outgroup a long projection appears as relatively plesiomorphous, and a short one, as in *Sphyraena* as apomorphous), 19 (relative length of lower jaw: apomorphous state of lower law protruding beyond upper jaw shared with *Scombrolabrax*) and 21 (presence of fangs, a characteristic *Sphyraena* shares with *Scombrolabrax*). The mugilids furthermore differ from *Sphyraena* in having a more apomorphous state for character 52 (two epurals, as opposed to three in *Sphyraena*).

Trichiuridae. According to Collette *et al.* (1984), the Gempylidae are a paraphyletic, more advanced sister group of the Trichiuridae. Johnson's (1986) hypothesis is that *Lepidocybium* is the primitive sister group to other gempylids, comprised of a monophyletic clade Gempylinae+Trichiurinae. Gago (1997, 1998) uses gempylids as outgroup for his cladistic analyses of trichiurids. The distribution of "Gempylinae" in the tree in which fossils are included, causes much confusion. In the tree without fossils, there seems to be one family Trichiuridae, in which the monophyletic Trichiurinae are a more specialised monophyletic crown group. Below the trichiurins, the trichiurids consist of the paraphyletic Gempylinae (Johnson's, 1986 Gempylinae, plus the fossil genera and *Lepidocybium*). Johnson (1986) mistakenly calls his gempylins+trichiurins clade Gempylidae, whereas Trichiuridae is preferred due to its older age (Trichiuridae Rafinesque-Schmaltz, 1810 *vs.* Gempylidae Gill, 1862). Danil'chenko (1962) and Parin & Bekker (1972) correctly group their Gempylidae and Trichiuridae in a suborder Trichiuroidei or Trichiuroidea. Although the Gempylinae as presented here are paraphyletic, the name is retained here for the sake of ease and convention. In the cladogram with fossils, some of the gempylins (*Thyrsites*, *Tongaichthys*, *Neoepinnula*, *Thyrsitops* and *Lepidocybium*) form, together with fossil taxa such as *Sphyraenodus* and *Wetherellus*, an unresolved sister group of the scombrids (it is interesting to notice at this point, that in the tree without fossils, the Scombrinae are the direct sister group of the trichiurids). Gempylins may be paraphyletic, but I have not come across a hypothesis in which they are split up into more than one polyphyletic group. I have no reason to believe that the gempylins are polyphyletic. Hence, I recognise for now the paraphyletic gempylins, which are the sister group to trichiurins in Fig. 8.2. A combination of poorly known, difficult to place fossils and the need to reinterpret the characters of the data matrix, probably resulted in the

disruption of the gempylins. The fossil *Progempylus*, normally considered a gempylin (Casier, 1966), has no clear phylogenetic position here. Because of its recurved conical teeth, however, its affinities are still most likely to be with the gempylins. The topology of the gempylins in the tree without fossils differs considerably from the cladogram of "gempylids" presented by Russo (1983). While *Lepidocybium* and *Ruvettus* are amongst the most basal "gempylids" in Russo (1983), here they are amongst the most advanced Gempylinae. In Russo (1983) *Rexea*, *Nealotus* and *Dicrotus* (as *Promethichthys*) form a monophyletic clade. In the provisional hypothesis presented here, *Rexea* is not closely related to either *Dicrotus* or *Nealotus*, although all three strongly resemble on the surface (see also Chapter 1). Here, *Thyrsitoides*, *Dicrotus*, *Nealotus* and *Nesiarchus* form a monophyletic group. The crown of three taxa of "gempylids" in Russo (1983) and the crown of three taxa of the Gempylinae here are identical: *Gempylus* as a sister taxon to the monophyletic clade *Diplospinus+Paradiplospinus*. The *Diplospinus+Paradiplospinus* clade is in turn the immediate sister group of the Trichiurinae. The topology of Gago's (1998) "trichiurid" cladogram differs from the topology of the Trichiurinae presented here. Unlike in Gago (1998), the monophyly of the eucaudate trichiurins is not supported here. *Trichiurus*, *Lepturacanthus*, *Eupleurogrammus* and *Tentoriceps* form the crown group of eucaudate trichiurids in Gago's cladogram. Here, the same taxa form a monophyletic clade with *Evoxymetopon*, which is a trichiurin with a caudal complex. In Gago (1998), *Evoxymetopon* forms a monophyletic clade with *Lepidopus altifrons* Parin & Collette, 1993. Gago's cladogram also implies that *L. altifrons* is not closely related to other species of *Lepidopus*. In the cladogram presented here, the fossil *Anenchelum* appears as the most primitive trichiurin and is not closely related to *Lepidopus*, with which it has mostly been confused. As in Gago (1998), *Aphanopus* is the most primitive Recent trichiurin. A major difference between my cladogram and Gago's is the position of *Benthodesmus*: one of the most basal "trichiurids" in Gago (1998) and one of the most advanced trichiurins here.

"*Euzaphlegidae*"/*cf. Gempylinae*. David (1943) and Danil'chenko (1960) discussed the scombroid suborder Euzaphlegidae, which contains amongst others *Thyrsion* and *Palimphyes*. That family does not appear as a monophyletic entity in the provisional scombroid cladogram. *Thyrsion* originates from a node that is the base of an unresolved bush, hence its phylogenetic position cannot be assessed at this point. *Palimphyes*, another member of the so-called Euzaphlegidae, forms a monophyletic clade with *Abadzekhia*, which is normally classified as a gempylid fish (Bannikov & Fedotov, 1989). Both *Abadzekhia* and *Palimphyes* share the peculiar apomorphy of enlarged and strongly overlapping dorsal pterygiophores

with gempylids and due to primitive characteristics such as large scales, should be basal trichiurids, and therefore gempylins.

Scombridae. In Collette *et al.* (1984), the Scombridae encompass *Gasterochisma*, Scombrini, Scomberomorini, Sardini and Thunnini. In Johnson (1986) *Gasterochisma* was excluded from the analysis. The other taxa that Collette *et al.* included in the Scombridae are also part of Johnson's scombrids and include, furthermore, also the billfishes. The composition of the scombrids in the cladogram that includes the fossil taxa is identical to that of Johnson (1986), plus a few fossil taxa. In the cladogram without the fossil taxa, the billfishes are distantly related to other scombroids, and the scombrids are paraphyletic. In the cladogram that includes the fossil taxa, I interpret the scombrids to be the clade above *Palimphyes* and *Abadzekhia*. The sister groups below the scombrids (from *Thyrsion* to *Abadzekhia*) are a mixture of gempylins and poorly known fossil taxa. Some of the subdivisions of the scombrids are highlighted below.

Scombrinae. The Scombrinae are normally understood to be the scombrid subfamily above *Gasterochisma* (see Collette, 1978; Collette *et al.*, 1984). Here, the tribe Scombrini is elevated to a subfamily Scombrinae. The level of subfamily was chosen, because the scombrins are in the first possible level of subdivision within the scombrids. In the consensus tree, *Scombrinus*, the Scombrinae (*Rastrelliger*, *Scomber*), *Tamesichthys*, *Eocoelopoma* and a monophyletic clade encompassing all other scombrids, all originate from the same node in the cladogram. On the surface, *Eocoelopoma* seems morphologically close to *Micrornatus*, but according to this provisional phylogeny they are not closely related. *Scombrinus* resembles *Scomber* and *Rastrelliger* in many aspects, differing from them by the closeness of their two dorsal fins and the possession of larger scales. In nine of the 12 most parsimonious trees, *Scombrinus* is the immediate sister group, or at least part of it, of *Scomber* and *Rastrelliger*.

Scomberomorinae. The Scomberomorinae are usually recognised as a natural entity, encompassing *Grammatorcynus*, *Acanthocybium* and *Scomberomorus* (see Collette & Russo, 1984). The fossils *Scomberodon*, *Palaeocybium* and *Neocybium* are also thought to be part of this group. According to Johnson's (1986), the Recent taxa are not closely related. According to that hypothesis, *Grammatorcynus* is the immediate primitive sister group of Sardini, *Scomberomorus*, *Acanthocybium* and billfishes. Within that crown group, *Scomberomorus* is the immediate primitive sister group of *Acanthocybium* and the billfishes. In this provisional cladogram, *Grammatorcynus*, *Scomberomorus*, Sardini, and a clade consisting of *Acanthocybium*, *Eothynnus* and billfishes originate from the same node.

Acanthocybium is here the sister taxon of *Eothynnus* and the billfishes. Johnson (1986) found that *Acanthocybium* is the direct primitive sister group of the billfishes. In the cladogram without fossil taxa, the Scomberomorinae, according to Collette & Russo (1984) form a monophyletic group. *Acanthocybium* shares apomorphies with Scomberomorinae, such as an elongated supratemporal groove, and also apomorphies with billfishes (mainly gill arch characters). The fossil *Eothynnus*, with its long supratemporal groove, multiple rows of small teeth and mid-lateral depressions in the vertebrae provide a link between *Acanthocybium* and billfishes. I favour here thus the *Acanthocybium*-billfish link, because it is strengthened by new data which have not before been used. Woodward (1901) thought that *Eothynnus* is almost identical to *Thunnus*, while Casier (1966) suspected that it is a scombrid that does not belong to the Thunnini. In the provisional cladogram, it appears as the immediate sister group of billfishes. A synapomorphy of the *Acanthocybium*+*Eothynnus*+billfishes clade is a long supratemporal groove. In billfishes, there is a reversal to a short supratemporal groove. A synapomorphy of the *Eothynnus*+billfishes clade is the possession of multiple tooth rows, with a further derived condition in Xiphiidae, where teeth disappear in adults. Although not identical, both *Eothynnus* and billfishes possess multiple rows of small tooth in their jaws. Woodward (1901) thought that *Eothynnus* is almost identical to *Thunnus*, while Casier (1966) suspected that it is a scombrid that does not belong to the Thunnini. In the provisional cladogram, it appears as the immediate sister group of billfishes. A synapomorphy of the *Acanthocybium*+*Eothynnus*+billfishes clade is a long supratemporal groove. In billfishes, there is a reversal to a short supratemporal groove. A synapomorphy of the *Eothynnus*+billfishes clade is the possession of multiple tooth rows, with a further derived condition in Xiphiidae, where teeth disappear in adults. Although not identical, both *Eothynnus* and billfishes possess multiple rows of small tooth in their jaws. The acanthocybiin *Palaeocybium* (not represented in the cladogram) also multiple (double) tooth rows. Although not included in the cladistic analysis, I believe *Palaeocybium* and *Scomberodon* are closely related to *Acanthocybium*, based mainly on dental morphology (see § 7.3). I recognise here that the Scomberomorinae are *Scomberomorus* and *Grammatorcynus*, based on that they form a monophyletic clade in the cladogram without fossils.

Sardinae Sardini and Thunnini are mostly understood to be monophyletic sister groups (Collette, 1978). In Collette *et al.* (1984) the various Sardini clades and a monophyletic Thunnini clade originate from the same node (Fig. 8.3). This tree topology does not guarantee that the Sardini are monophyletic. Johnson (1986) treated "Sardini" and Thunnini" as one single clade. His nomenclature is somewhat confusing, since he mentions in his classification that there is one clade, called

Sardini, which encompasses both Sardini and Thunnini. Johnson did not report on the resolution of genera within his single Sardini clade. In this hypothesis, the endothermic, more advanced Thunnini appear as the crown group of a clade, which otherwise consists of a more primitive, paraphyletic clade of Sardini. Together, the Sardini and Thunnini form the monophyletic Sardinae, which is equivalent to Johnson's Sardini. The Sardini are paraphyletic in the hypothesis presented here, but the name Sardini is retained for the sake of ease and convention. *Orcynopsis* and *Cybiosarda* are normally understood to be closely related, but in the proposed cladogram that is not the case. Monsch (2000) suggested that a new fossil *Gymnosarda*, *G. prisca*, provides evidence that *Gymnosarda* is a link between Sardinae and Scomberomorinae, because *G. prisca* is the only member of Sardinae that possesses a large caudal notch, as in the Scomberomorinae. The proposed cladogram is not explicit in that respect, since Sardinae and the Scomberomorinae originate from the same node. When mapping the hypural fusion pattern on the cladogram in MacClade, it is shown that the state of this character at the above mentioned node is equivocal. It seems parsimonious though, that the basal node of the Sardinae has the character state of a large caudal notch, which is strongly reduced within *Gymnosarda* and ultimately disappears in its advanced sister taxa. Hence, it seems that this cladogram supports the evolutionary scenario of the caudal notch as described in Monsch (2000). This cladogram supports the evidence that Graham & Dickson (2000) supply to include *Allothunnus* in the Thunnini rather than Sardini. In cladograms of Collette (1978) and Collette *et al.* (1984), *Auxis* and *Euthynnus* form a monophyletic clade, as do *Thunnus* and *Katsuwonus* (Fig. 8.3). In the provisional cladogram however, the topology above *Allothunnus* is different from that in the above cited references. Here, the relationships of the Thunnini above *Allothunnus* are poorly resolved. *Katsuwonus* and *Euthynnus* form a monophyletic clade. Bannikov (1985) suggested that *Palaeothunnus* is a primitive member of the "Thunninae" (equivalent to Sardinae as defined here). In the proposed cladistic hypothesis, *Palaeothunnus* appears as the sister group to *Grammatorcynus*, *Scomberomorus*, Sardinae, *Acanthocybium*, *Eothynnus* and billfishes.

Billfishes. According to Collette *et al.* (1984), the billfishes are the direct primitive sister group of the scombrids. According to Johnson (1986), the billfishes are amongst the most advanced scombrids, with *Acanthocybium* as their immediate sister group. Finnerty & Block (1995) showed that, on the scale of the taxa they investigated, the cytochrome-*b* gene of billfishes shows an only distant resemblance with those of scombroids. If their gene tree is to be taken as a taxon tree, then billfishes would be a sister group to scombroids. In this study, I found evidence that supports that billfishes are more parsimoniously placed within the

scombroids. As in Johnson's hypothesis, the billfishes appear as an advanced clade within the scombrids. In all the performed PAUP* analyses, the fossil billfishes form a monophyletic clade with Recent billfishes. *Blochius* is closely related to *Xiphias*, with which it shares characters such as the absence of pelvic fins and a flattened bill (although it is more flattened in *Xiphias*). *Blochius* superficially resembles as *Xiphias* larva. The large scales of *Blochius* resemble those of larval and juvenile *Xiphias*. Istiophorini and Palaeorhynchini appear as sister groups. Even though the billfishes as a whole share a remarkable apomorphy with *Coryphaena* (one continuous soft dorsal fin) and palaeorhynchins share remarkable apomorphies with *Coryphaena* (number of vertebrae, first anal pterygiophore not articulating with first haemal spine, modified preural spines), the palaeorhynchins do not appear to be closely related to *Coryphaena*. As outlined above, the billfishes appear to be distantly related to other scombroids in the cladogram without fossils, and appear as a clade within the scombrids, because of the inclusion of *Eothynnus*.

Fossil taxa. The inclusion of fossil taxa has different impacts on resolution of the clades and monophyly in the cladograms. All the fossil taxa contained in the analysis have a unique set of characters, which was revealed by the safe taxonomic deletion algorithm TAXEQ2. However, the main impact that the fossils make in the cladogram, is loss of resolution. I suspect that part of the reason for that is the need to re-interpret the characters used for the cladistic analysis. The analysis without fossils also put a great strain on the memory of PAUP*. Many of the fossils are known mainly from cranial characters. *Progempylus*, normally considered a gempylin fish, has no clear phylogenetic position. The inclusion of fossils seems to make the gempylins polyphyletic. On the other hand, the fossils seem to make the scombrids monophlyetic, while they are paraphyletic in the cladogram without fossil taxa. If the fossils are not considered, the paraphyletic gempylins and monophyletic trichiurins form a monophyletic family Trichiuridae. *Anenchelum* is here recognised as the most basal trichiurin, providing a link between other trichiurins and the paraphyletic gempylins, not breaking the relationship between the trichiurins and the *Paradiplospinus+Diplospinus* clade, but rather confirming it. The phylogenetic positions of *Palaeothunnus* and *Godsilla* as relatively primitive scombrids seem well resolved. *Eothynnus* provides a link between *Acanthocybium* (here not recognised as a scomberomorin), and the billfishes. The phylogenetic position of the fossil billfishes also seems well resolved. Palaeorhynchins share remarkable apomorphies with *Coryphaena*. However, the billfishes, as pictured in Fig. 8.1 always appear in a monophyletic clade, which is more parsimoniously placed in the ingroup rather than in the outgroup. Improvement of the character analysis should also improve the resolution of the

cladogram that includes fossils. However, I can foresee that more taxa will have to be deleted to improve resolution. If that is necessary, a sound methodology has to be devised to decide which taxa to exclude.

Endothermy. Block *et al.* (1993) were the first to state that scombroid endothermy has evolved three times separately, a conclusion they came to after mapping physiological traits of scombroids on a cladogram of the cytochrome-*b* gene of scombroids. Even though it was the first time evidence was supplied to support three separate appearances of endothermy, Johnson & Baldwin (1994) argued that Block *et al.*'s hypothesis was not needed to postulate those three separate appearances, and that his own (Johnson, 1986) phylogenetic hypothesis can be used to come to the same conclusion. However, Johnson did not include *Gasterochisma* in his final analysis and does not make a phylogenetic distinction between ectothermic Sardini and endothermic Thunnini. In their argument, Johnson & Baldwin (1994) assign (although with hesitation) to *Gasterochisma* the phylogenetic position it would have occupied if included in Johnson's (1986) analysis, and repeated Johnson's (1986) assumption of a close relationship between Sardini and Thunnini. As part of the cladistic analysis, I have investigated the evolution of endothermy in scombroids. Rather than mapping physiological traits on the cladogram of a single gene or on a morphological tree, osteological and anatomical characteristics that evidence endothermy are used as characters in the matrix. For the first time, characteristics which express the form and degree of endothermy have been used in an analysis to investigate the nature of its evolution in scombroids. Unfortunately, none of the fossil taxa possesses (new) characters that give new insights on the evolution of endothermy, and one of the endothermic taxa, *Gasterochisma*, has been deleted from the eventual analysis. The types of heater system of the endothermic taxa that were part of the analysis are mapped on the cladogram (Figs. 8.1, 8.2). Although it is not clear if *Allothunnus* is endothermic, the anatomical structures that could cater for body warming are in place (Graham & Dickson, 2000). There is no structural evidence of endothermy in fossil billfishes. Character mapping in MacClade showed that endothermy in scombroids (excluding *Gasterochisma*) has evolved on two separate occasions. Within the Thunnini, the neothunnoid heater evolves into the thunnoid heater in *Thunnus subg. Thunnus*. The two endothermic groups are not closely related. It seems unlikely, using the parsimony principle, that endothermy has evolved at the node above *Palaeothunnus* (Fig. 8.1) and then to be reversed in most taxa, except for Thunnini and billfishes, both in which it then should develop in rather diverging directions. Since *Gasterochisma* is not in the cladogram, it is not possible to state what place this genus has in the evolution of scombroid endothermy (if a scombroid at all). It would be interesting if *Gasterochisma* came out to be closely

related to either billfishes or Thunnini. If *Gasterochisma* belongs to the scombroids, endothermy could have evolved either twice or three times independently in this group. In the cladogram without fossils, the relationships between the endothermic groups are different, but endothermy also seems to have evolved twice separately in that case. The finding that endothermy in billfishes and Thunnini has evolved twice separately does not differ from what Block *et al.* (1993) implied.

8.5.2. Brief overview of character evolution

I do not deem it worth while to present a detailed survey of synapomorphies of every node in a preliminary hypothesis that needs reworking. Thus, I present a brief summery of a few selected clades. I present a list of synapomorphies of scombroids, trichiurids, trichiurins, scombrids, sardins, Thunnini, *Acanthocybium*+*Eothynnus*+billfishes, *Eothynnus*+billfishes and billfishes. The reason for presenting a list of scombroid synapomorphies is obvious. The trichiurids and trichiurins are chosen because of the intriguing hypothesis that trichiurins are advanced gempylins. The Sardinae and Thunnini are chosen for the same reason (Thunnini being advanced sardins). The billfishes are chosen to assess the characters that define this assembly of Recent and fossil taxa, and their character evolution related to their direct sister groups, as found here (*Acanthocybium* and *Eothynnus*) is assessed.
Character state changes are based on character tracing in MacClade. Except for the Trichiuridae, this overview is based on the cladogram in Fig. 8.1 (see below).

Scombroids. **Character 11, state 1.** In the primitive state, the supramaxilla is present. In the outgroups lower than "mugilids", the supramaxilla is absent. The presence of the supramaxilla, a reversal, is a synapomorphy of the outgroup taxa above the "mugilids" and the scombroids. In billfishes above *Xiphiorhynchus* the supramaxilla is missing again. **Character 12, state 1.** The non-protrusibility of the upper jaw is a synapomorphy of the scombroids. This trait also appears independently inn *Luvarus* and *Sphyraena*. **Character 29, state 1.** The unique articulation of the second epibranchial with the third pharyngobranchial. **Character 30, state 1.** Fourth pharyngobranchial cartilage absent. **Character 33, state 1.** Number of gill rakers greatly reduced at the base of scombroids. In some groups (trichiurins, *Lepidocybium*, billfishes, *Acanthocybium*), the gill rakers are missing and in Scombridae below the billfishes there is a reversal towards gill arches fully occupied by spinescent gill rakers. **Character 35, state 1.** Posterodorsal notch in operculum, at the base of the scombroids. In some groups there is a reversal towards the absence of this notch. **Character 38, state 1.**

Number of vertebrae 28-64 (also appears in outgroup taxon *Coryphaena*). In trichiurins this state is more advanced, in that they have between 67 and 174 vertebrae. In Recent billfishes there is a reversal towards a vertebral count of 23-36. **Character 56, state 1.** The absence of the procurrent spur is a synapomorphy of scombroids and also appears in the outgroup taxa except *Scombrolabrax* and *Sphyraena*. **Character 60, state 1.** Predorsal bones are absent in all scombroids and *Coryphaena*. **Character 61, state 1.** At the base of scombroids, the first dorsal pterygiophore is inserted in the first or second interneural space. There is a reversal towards insertion in the third interneural space in many groups.

Trichiuridae. In the cladogram with fossils (Fig. 8.1), the trichiurids appear as a paraphyletic group. Synapomorphies of the monophyletic trichiurids in the cladogram without fossils (Fig. 8.2) are given here. **Character 19, state 2.** Lower jaw protrudes beyond upper jaw. This trait also appears in *Sphyraena* and *Scombrolabrax*. **Character 21, state 1.** Presence of premaxillary and dentary fangs. This trait also appears in *Scombrolabrax* and *Sphyraena*. **Character 23, state 1.** Serial teeth retrorse. In the trichiurins, there is a reversal towards straight serial teeth. **Character 50, state 2.** Hypural plate formula at the base of trichiurids is 1+2, 3+4, 5. Several reversals to state 0 and 1 occur within this group. **Character 62, state 1.** Modified configuration of dorsal pterygiophores: strongly overlapping and elements interlinked. **Character 70, state 1.** Second dorsal fin spine present, with reversal to absence in *Paradiplospinus* and parallel appearance in *Katsuwonus* and *Trachurus*, *Sphyraena* and "muglilids". **Character 80, state 2.** Larvae with a set of unique synapomorphies: deep, serrated dorsal spine, short but precocious. In trichiurins the larvae seem more advanced in that their first dorsal is less deep, the pelvics are smaller and the preopercular spine missing. This is in accordance with Johnson (1986), but contradicts with my earlier assessment (Chapter 5) that gempylin larvae are more advanced than those of trichiurins. Trichiurins are also characterised by reversals in characters 30, 45, 47 and 49.

Trichiurinae. **Character 1, state 1.** The gempylins show a mixture of lachrymal sizes, but all trichiurins have lachrymals that are longer than the orbit diameter. **Character 24, state 1.** One single pair of nostrils as opposed to two pairs. **Character 33, state 2.** No splint-like gill rakers. This trait also occurs in *Nesiarchus*, *Acanthocybium* and Recent billfishes. **Character 36, state 1.** Opercular elements fimbriated at the margins. **Character 38, state 2.** Vertebral count 76-174. **Character 52, state 2.** One epural. **Character 63, state 1.** Soft dorsal pterygiophores fully associated with neural spines. Reversal in *Benthodesmus*. **Character 69, state 1.** At the basis of trichiurins, the number of second dorsal fin rays is between 29 and 85. Above *Assurger* this count is 98-142

(state 1) with a reversal to state 2 in *Evoxymetopon*. Apparently, this character evolved differently than in my assessment in Chapter 5, where I concluded that a high second dorsal fin ray count is the plesiomorphous state. **Character 71, state 1.** Soft dorsal pterygiophores consist of three autogenous radials as opposed to two in other groups. **Character 80, state 2.** See on trichiurids above.

Scombridae. **Character 27, state 1.** Ceratohyal window present at base of scombrids. Reversals occur in billfishes, Scombrinae, Thunnini and within genus *Sarda*. **Character 31, state 1.** Triangular stay from 4th pharyngeal tooth plate to 3rd pharyngobranchial. A reversal occurs in *Grammatorcynus*, where this stay is absent. **Character 48, state 1.** Two pairs of fleshy lateral caudal keels. A reversal occurs in *Xiphias*, where these keels are missing. **Character 53, state 2.** At the base of the scombrids, the hypural plate formula is 1+2, 3+4, 5. Several more advanced states have subsequently evolved within this group. **Character 75.** Pelvic plate well developed, with three differentiated wings. In *Xiphias*, the pelvic plate is missing. Hypurostegy (**character 51, state 1**) is normally considered a synapomorphy of scombrids, but the caudal fin of *Eocoelopoma* is not hypurostegic and the caudal region of *Tamesichthys* is unknown. Scombrids are also characterised by reversals in characters 38 and 64.

Sardinae. **Character 43, state 1.** Preural vertebrae abruptly shortened. This trait also appears in *Palaeothunnus*. **Character 47, state 2.** Mid-lateral fleshy caudal keel well developed. This trait also occurs in *Xiphias* and *Luvarus*. **Character 53, state 4.** Hypurals 1-4 fused, caudal notch present. The notch disappears within *Gymnosarda* and in the Sardinae above *Gymnosarda*. **Character 54, state 4.** Fifth hypural partially fused to hypural plate. This condition also occurs in *Lepidopus*, *Lepidocybium* and *Eocoelopoma*. **Character 76, state 1.** Dark muscle tissue migrated away from outer surface of myotome towards axial skeleton. In Thunnini the dark muscle surrounds the vertebral column (state 2). **Character 79, state 3.** Anterior corselet present, rest of the body naked or almost.

Thunnini. **Character 10, state 2.** Long posterior intercalary projection. In *Thunnus* there is a reversal to state 0 (projection absent). **Character 17, state 1.** Cartilaginous ridges on tongue. **Character 76, state 2.** Dark muscle tissue surrounds spinal column.

Acanthocybium+Eothynnus+billfishes. **Character 2, state 1.** Supratemporal groove extends anteriorly to anterior tip of frontal. In billfishes, the supratemporal groove is absent (state 2). **Character 16, state 1.** Larval beak elongated and horizontally orientated (state in fossils unknown, but assumed by MacClade).

These elongated larval beaks also occur in *Thyrsites* and *Gymnosarda*. **Character 32, state 1**. Gill filaments modified with interconnections and denticles (state in fossils unknown, but assumed by MacClade). **Character 33, state 2**. Spinous gill rakers absent (assumed in fossils by MacClade)

Eothynnus+billfishes. **Character 20, state 3**. Multiple rows of minute teeth in dentary and premaxilla. In the palaeorhynchins, the number of tooth rows in uncertain. The xiphiins are edentate (state 4). This clade is also characterised by a reversal in character 27 (no ceratohyal window). This trait also occurs in trichiurins, *Lepidocybium* and *Nesiarchus*.

Billfishes. **Character 2, state 2**. Supratemporal groove absent. A reversal occurs in *Blochius* and *Xiphias*, where a short supratemporal groove is present. The supratemporal **Character 18, state 1**. Upper jaw developed into rostrum with ovoid transverse cross-section. In *Xiphias* and *Blochius* the rostrum is more flattened (state 2). groove is also missing in *Luvarus* and the "mugilids". Billfishes are also characterised by a reversals in characters 6 (no cranial crest), 11 (no supramaxilla). **Character 19, state 1**. Rostrum more than twice as long as lower jaw. In *Tetrapturus* and there are species with shorter rostra, and in the *Palaeorhynchus*, *Pseudotetrapturus* and *Blochius*, lower and upper jaw are of almost equal length because the lower jaw is also elongated (reversal to state 0). Several synapomorphies of billfishes, such as soft first dorsal fin rays cannot be used to characterised the billfishes as defined here, because of missing entries in certain fossil taxa.

CHAPTER 9: RECAPITULATION

9.1 Discussion and suggestions for further research

Although a conclusive phylogenetic hypothesis of scombroids has not been presented, the results are encouraging and interesting.

Adding fossils to the phylogenetic study of scombroids has led to mixed results. On the one hand, some phylogenetic hypotheses are confirmed or strengthened and others rejected. On the other hand, many of the fossil taxa seem to negatively influence the degree of resolution in the cladograms. *Acanthocybium* appears to be more closely related to the billfishes than to the Scomberomorinae. This hypothesis is strengthened by the inclusion of *Eothynnus*, of which only the cranial region known. In the phylogenetic hypothesis without fossils, the trichiurins appear as advanced gempylins. The inclusion of the fossil trichiurin *Anenchelum* did not alter that relationship; it appears here as the most primitive trichiurin. The Scombridae are a paraphyletic group in the hypothesis without fossils, but are monophyletic in the hypothesis with fossils. Although all the included fossil taxa had unique character combinations, many of them do not contribute in a positive way towards a well-resolved cladogram. Although the fossils present a unique combination of data, many have a great number of missing entries in the data matrix and are thus still difficult to place. If the taxon however has the "right" combination of preserved characters, it can provide interesting information, as is the case for *Eothynnus*.

Prior to the cladistic analysis, some fossil taxa had been deleted according to Safe Taxonomic Deletion (STD) rules using the computer program TAXEQ2. According to that algorithm, only two taxa show full equivalence and can thus be safely deleted. However, the algorithm does not take into account characters that are not parsimony-informative. *Palaeocybium*, for example was safely deletable because it has a dental character that is plesiomorphous compared to that in *Acanthocybium* and shares with *Acanthocybium* a character that is parsimony uninformative according to PAUP*. It could be that many of the fossils included in the analysis could still be safely deleted, even though they do not show total equivalence according to TAXEQ2. *Palaeocybium* slipped through the mazes of the Safe Taxonomic Reduction algorithm, and maybe others have as well, for reasons yet unknown. I would suggest that the algorithm of TAXEQ2 to be expanded, to at least take parsimony uninformative characters into account. If these characters are removed from the analysis, some taxa that did not show total equivalence might do then. There are a few options, such as implementing an STD algorithm in programs that may detect characters that are parsimony uninformative, such as PAUP* and MacClade, so that these uninformative characters are

overlooked, or one could write a batch file that can be linked to PAUP* and which instructs PAUP* to determine which taxa are safely deletable, hereby also recognising uninformative characters. Autodecay (Eriksson & Wikström, 1996), a program that calculates decay indices is exactly that: a program into which one introduces tree files and parameters, after which it instructs PAUP* to calculate the decay indices.

The Reduced Cladistic Consensus method, or RCC (Wilkinson, 1994) was devised to recognise taxa that display alternative equally parsimonious possible positions (underdetermined taxa), prune those from the tree structure, and calculate a consensus tree that expresses all positive statements of relationships expressed in the population of most parsimonious trees. Fossil taxa with many missing data could easily be underdetermined. Hence, I supposed that the RCC method would be a useful tool to express the information the multiple parsimonious trees from my data have in common. However, the strict reduced consensus tree I produced showed only little resolution. This may be because the strict reduced consensus method is partially based on the strict consensus method. There are hardly any resolved nodes in the strict consensus tree, and if a reduced strict consensus is based on the backbone of a strict consensus, the result might not be well resolved either. I do not think that the poor performance of RCC in this case is caused by faults in the methodology. RCC has already proved its worth in producing better resolved consensuses (Wilkinson & Benton, 1995 and 1996). Rather, the poor performance of RCC is an indication that the data set needs reworking before it can produce robust results.

As said above, the data set, as presented here, is problematic and I do not believe that the cladograms I produced (Figs. 8.1, 8.2) correctly express all scombroid relationships. Here, I propose some solutions to better represent the information I extracted, either directly from specimens or from literature references.

In my attempt to keep the data matrix compact and concise, I introduced many multistate characters. However, these multistate characters also increase the average number of evolutionary steps per character. Multistate characters also represent more complicated evolutionary scenarios than when the character is split into several binary characters. Another reason for creating many multistate characters was to eliminate the number of non-applicable character states. One could, for example, include in every character related to the pelvic fin introduce a character state "pelvic fin absent", or create a character that expresses presence or absence of the pelvic fin. Subsequently, all pelvic characters for taxa without pelvic fins can be coded as non-applicable (in effect, that is the same as character state "missing"). Although that creates more missing entries and more characters to work with, the

evolutionary picture painted looks somewhat clearer, which in the case of the scombroid data will hopefully improve the solvability of the hypotheses.

I feel as well that there are some characters that do not add new information and can be safely deleted, while retaining all the necessary information that expresses the relationships. For example, the Trichiurinae are presented here as being characterised by 10 synapomorphies, and Sardinae by six. I feel that for this cladistic analysis, some of these synapomorphies may be deleted from the analysis, so that monophyletic clades are still retained, but then supported by a lesser number of synapomorphies. The deletion of those characters could improve the performance of the heuristic searches, and is also a counterbalance against the creation of more characters on the other hand, by splitting multistate characters into binary ones.

Some characters will simply require reinterpretation. An example is the characters related to dorsal fins, second dorsal fins and finlets. In my first assessment, I hypothesised that a long continuous dorsal fin consisting of many soft rays is the plesiomorphous state, and that the second dorsal of billfishes is split off this fin. Subsequently, this second dorsal evolves into the finlets of the other scombrids and a reduced number of (second) dorsal fin rays is a further derived condition. However, as described in § 8.5.2, a higher number of dorsal fin elements seems to be the more derived state within the trichiurids. Also, as expressed in Fig. 8.1, the billfish arise from within scombrids with finlets, thus their "second dorsal" seems to be derived from finlets and not the other way round (that is, if these structures are homologous at all). The nature of characters such as these need to be better understood before they are adequately represented in the data matrix.

Further research into scombroid relationships in the more distant future can benefit from a number of possible research options.

More molecular analyses can be conducted on scombroids, using different material than the cytochrome-*b* gene, and one can observe if these provide results that are consistent, that are consistently different from morphological hypotheses or if they favour one hypothesis more than another. It would also be interesting to combine as much evidence as possible in total evidence analysis, in which cladistic hypotheses are drawn from matrices possessing, molecular, morphological (if possible, morphological data from fossil taxa can be included). In that case, all possible sources of evidence are combined, which is, as far as I am concerned a fully justified approach, if the methodologies to produce these total evidence phylogenies are sound.

Histological studies of bones may provide supplemental data on the endothermy of certain taxa, and comparison with ectothermic taxa. If that proves to

be successful, one could assess whether certain fossil scombroids were endothermic or ectothermic.

Investigation of more specimens, especially of lesser known taxa such as *Rexichthys* could provide more information. I do not know if *Gasterochisma* is a scombroid, this study is inconclusive in that respect. More data of this taxon, or an investigation of *Gasterochisma* from a new angle might shed new light on the affinities of this enigmatic taxon. There is more unstudied and/or long time ignored fossil scombroid material, housed in institutes in amongst others Russia, Belgium, Japan, Romania, France and Italy, which could supply additional information.

9.2 Conclusions

The conclusions on phylogenetic relationships only preliminary and should be taken only as interesting results that still need confirming and can still be rejected.

Sphyraena is not a scombroid, and is used here as an outgroup taxon of scombroids. Within the framework of those outgroup taxa *Sphyraena* does not appear to be closely related to the Mugilidae, as might be expected, but more closely to *Scombrolabrax*. The exclusion of *Sphyraena* from scombroids contradicts Johnson's (1986) finding that *Sphyraena* is a member of the Scombroidei and further supports molecular evidence of Finnerty & Block (1995) that *Sphyraena* is not a scombroid.

Billfishes are found to be scombroids, thus rejecting molecular evidence (Finnerty & Block, 1995) that billfishes might be only distantly related to the mackerel-like fishes. The billfishes are found to be amongst the most advanced scombrids with *Acanthocybium* as one of their most immediate sister groups. This is in accordance with Johnson's (1986) findings and rejects that of Collette *et al.* (1984) that billfishes are primitive scombroids and a sister group of scombrids. Palaeorhynchins, *Xiphiorhynchus* and *Blochius* are part of a monophyletic clade of billfishes. *Blochius* and *Xiphias* form a monophyletic clade. The immediate sister taxon of the billfishes is *Eothynnus*. The supposed fossil billfish *Acestrus*, *Cylindracanthus*, *Enniskellinus* and *Hemirhabdorhynchus* are here considered not to be billfish, but their systematic status remains uncertain. *Aglyptorhynchus* is probably a billfish, but I feel that more information is needed to confirm or definitely reject this.

The Trichiuridae are a monophyletic group, at the base consisting of the paraphyletic Gempylinae and the monophyletic Trichiurinae as crown group. This

arrangement differs from any other known phylogenetic hypothesis. In Collette *et al.* (1984) the Trichiuridae are the sister group of all other scombroids, with the Gempylidae at the base of that clade. In Johnson (1986), *Lepidocybium* is the sister group of a clade which consists of a perfect dichotomy between Gempylinae and Trichiurinae. Within the gempylins, I had been struck by the similarities between *Dicrotus* (the correct name for what is currently better known as *Promethichthys*), *Rexea* and *Rexichthys*. However, the three genera are genera in their own right and are not lumped. Although *Dicrotus* is superficially the most similar to *Rexichthys*, it appears to be more closely related to *Nesiarchus* and *Nealotus*.

The Sardinae are a monophyletic group, with at the base the paraphyletic Sardini and the monophyletic Thunnini as crown group. In Collette *et al.* (1984) the Sardini and Thunnini form a perfect dichotomy (that is, if *Allothunnus* is there recognised as a thunnin). In Johnson (1986) the Sardini and Thunnini form one monophyletic group (which is, bizarrely, also called Sardini), but the internal structure of that group is not given. *Gymnosarda* is the most basal sardin, being the only one of that group that has at least one species with a large caudal notch. In the Recent *Gymnosarda*, *G. unicolor*, there is still a vestigial remnant of that notch. *Allothunnus* is a member of the Thunnini, thus supporting the findings of Graham & Dickson (2000). *Palaeothunnus* is not closely related to the Thunnini, but is the most basal scombrid above the Scombrinae. *Eothynnus* is the direct sister group of the billfishes.

The phylogenetic position of many of the fossil scombroids is yet unresolved. Many of them lower the degree of resolution in the scombroid cladogram, but some, such as *Eothynnus*, *Anenchelum* and the fossil billfishes have provided much useful information. Several taxonomic revisions have been made about the fossil scombroids. It would go to far to mention them all in this section of conclusions.

When excluding *Gasterochisma*, endothermy has evolved twice independently in the Thunnini and in the billfishes. If *Gasterochisma* is a scombroid, endothermy has evolved at least twice independently and at most three times.

THE END

"And in the end

The love you take

is equal to the love you make"

(Lennon & McCartney, 1969)

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APPENDIX 1: LIST OF SPECIMENS

†*ABADZEKHIA*

A. marinae

PIN 1413-81, **Holotype**, river Belaya[7], near Abadzekhskaya village, Caucasus, Russia, Upper Oligocene: Chattian (Morozkina Ravine Horizon).

PIN 1413-82 (two counterparts, one of which is transfer prepared), **Paratype**, river Belaya, near Abadzekhskaya village, Caucasus, Russia, Upper Oligocene: Chattian (Morozkina Ravine Horizon).

PIN 1413-83, **Paratype**, river Belaya, near Abadzekhskaya village, Caucasus, Russia, Upper Oligocene: Chattian (Morozkina Ravine Horizon).

ACANTHOCYBIUM

A. solandri

BMNH 1879.10.28.1, Atlantic, Recent skull.

BMNH 1965.12.1.104 (labelled as *Scomberomorus commersoni*), off Egg Island, St. Helena, spirit specimen.

BMNH 1965.12.1.105, off Egg Island, St. Helena, spirit specimen.

USNM 270393 (see also Colette & Russo, 1984), 21°50'N, 86°34'W, Atlantic, Recent.

USNM 270394 (see also Collette & Russo, 1984), Halfway between "Oregon 3611-12" and Bluefield, Nicaraguan Shelf, Caribbean, Recent skeleton.

USNM 270396 (see also Collette & Russo, 1984), Arabian Sea, Indian Ocean, Recent skeleton.

USNM 270397 (see also Collette & Russo, 1984), San Benedicto, Isla de Revillagigedos, Pacific, Recent skeleton.

USNM 270398 (see also Collette & Russo, 1984), NW Indian Ocean, Recent skeleton.

USNM 270399 (see also Collette & Russo, 1984), off Miami, Florida, U.S.A., Recent skeleton.

USNM 270403 (see also Collette & Russo, 1984), 11°40'N, 83°9'W To 11°37 N, 83°10'W, off Nicaragua, Caribbean, Recent skeleton.

†*A. sp.*

BMNH P14029 (vertebra), Barton, Hampshire, England, Bartonian (Barton Clay). Some items catalogued under this number are described under *Scomberomorus excelsus* and *Scomberodon*.

USNM 286420, (labelled "probably not Istiophorid ?Wahoo"), no data, fossil hypural plate.

USNM various uncataloged specimens, (some labelled as *Acanthocybium* sp, as *A. solandri*, or not labelled), South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Miocene (Fish Stratigraphic Column, Pungo River Formation).

†*cf. ACANTHOCYBIUM*

BMNH P27010 (labelled *Scomberoides*), Sheppey, England, Ypresian (London Clay).

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7 Belaya rechka, here translated river Belaya, literally means "White river".

PIN 1878-2, Western extremities of Ustyurt Plateau, Kazakhstan (Shorym Svita), Upper Eocene: Priabonian (**paratype** of *Scomberomorus saevus*) USNM 2667, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., hypural plate, Early Pliocene: Zanclean (Yorktown Formation).

USNM 498663, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., hypural plate, Early Pliocene: Zanclean (Yorktown Formation).

USNM 498667, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., hypural plate, Early Pliocene: Zanclean (Yorktown Formation).

USNM 498668, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., hypural plate, Early Pliocene: Zanclean (Yorktown Formation).

USNM 498669, South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., hypural plate, Miocene (Fish Stratigraphic Column, Pungo River Formation).

USNM 498672 South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., hypural plate, Early Pliocene: Zanclean (Yorktown Formation).

USNM 498673, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., hypural plate, Early Pliocene: Zanclean (Yorktown Formation).

†ACESTRUS

A. ornatus

BMNH 627, **Holotype**, Sheppey, England, Ypresian (London Clay).

BMNH P1793, Sheppey, England, Ypresian (London Clay).

BMNH P60905, Sheppey, England, Ypresian (London Clay).

†AGLYPTORHYNCHUS

A. venablesi

P27612-4 (**Paratypes**), Bognor Regis, Sussex, England, Ypresian (Fish tooth bed of London Clay).

BMNH P27615 (**Holotype**) Bognor Regis, Sussex, England, Ypresian (Fish tooth bed of London Clay).

†ANENCHELUM

A. glarisianum

BMNH 41807, (labelled as *Lepidopus*) Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

BMNH 41808 (labelled as *Lepidopus glarisianus*) Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

BMNH 41812 (labelled as *Palaeorhynchus* sp.), Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

BMNH P442, (labelled as *Lepidopus*), **Holotype** of *Anenchelum isopleurum*, Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

BMNH P451 (labelled as *Lepidopus*), Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

BMNH P1711, Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

BMNH P3994 (labelled as *Anenchelum latum*), Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

BMNH P40132 (labelled as *Lepidopus* sp.), Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

BMNH P65193 (labelled as "*Ananchelum* sp."), Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

PIN 1413-88 (catalogued as *Lepidopus glarisianus*), river Belaya, Caucasus, Russia, Lower Oligocene: Rupelian (Khadum deposits).

PIN 1413-93 (catalogued as *Lepidopus*), river Belaya in Abadzekhskaya village, Caucasus, Russia, Lower Oligocene: Rupelian (Lower Khadum Horizon).

PIN 1413-94, **Holotype** of *Lepidopus angustus*, river Belaya, Russia, Caucasus, Lower Oligocene: Rupelian (Khadum deposits).

PIN 3363-17, **Paratype** of *Lepidopus angustus*, river Belaya, Caucasus, Russia, Lower/Middle Oligocene (Khadum deposits).

PIN 3363-143 (labelled as *Anenchelum angustum*), river Belaya, North Caucasus, Russia, Lower Oligocene: Rupelian.

PIN 3363-144 (labelled as *Anenchelum angustum*), river Belaya, North Caucasus, Russia, Lower Oligocene: Rupelian.

A. paucivertebrale

PIN 4425-23, **Holotype**, river Pshekha, near village Gornyy Luch (Krasnodar territory), Cuacasus, Russia, Middle Eocene (Bartonian, Kuma Horizon).

PIN 4425-24, **Paratype**, river Pshekha, near Gornyy Luch village (Krasnodar territory), Cuacasus, Russia, Middle Eocene (Bartonian, Kuma Horizon).

PIN 4425-25, **Paratype**, river Pshekha, near Gornyy Luch village (Krasnodar territory), Cuacasus, Russia, Middle Eocene (Bartonian, Kuma Horizon).

PIN 4425-28, river Pshekha, near Gornyy Luch village (Krasnodar territory), Caucasus, Russia, Middle Eocene (Bartonian, Kuma Horizon).

†cf. ANENCHELUM

Anenchelum? eocaenicum

PIN 1413-78, **Holotype**, catalogued as *Lepidopus*, Tbilisi, Georgia, Middle Eocene (Dabakhansk Svita).

"Lepidopus glarisianus"

BMNH 41811, (labelled as *Lepidopus glarisianus*) Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

APHANOPUS

A. carbo

BMNH 1855.12.26.390, Madeira, Portugal, Recent skeleton.

BMNH 1899.1.10.15, Recent skeleton.

BMNH 1899.1.16.5, no data, Recent skeleton.

BMNH 1961.6.20.1, no data, spirit specimen (x-rayed).

BMNH uncat., No data, Recent skull.

†A. sp.

BMNH P10444, Copiapo, Chile, Upper Tertiary.

†ARDIODUS

A. mariotti

BMNH P2660-4, Sheppey, England, Ypresian (London Clay).

BMNH P14809 (labelled as *Eocoelopoka colei*), Upnor, Kent, England, Upper Palaeocene: Thanetian (Oldhaven Beds).

BMNH P38281-3 (labelled as *Eutrichiurides goberti*), Morocco, Thanetian-Ypresian (Phosphates).

BMNH P42689, Bognor Regis, England, Ypresian (Lower Fish-tooth Bed, London Clay).

AUXIS

A. thazard thazard

BMNH 1897.4.6.74, N. Celebes, Indonesia, spirit specimen (x-rayed).

A. rochei

BMNH 1967.21.1:272-274, ANtelais Saghir Frontage, spirit specimens.

A. sp.

KAM 2 ("Jude"), purchased from fishmonger, Bristol, 1996.

KAM 3 ("Eleanor"), purchased from fishmonger, Bristol, 1996.

BENTHODESMUS

B. simonyi

BMNH 1906.11.30.49, Cezimbru, Portugal, spirit specimen (x-rayed).

BMNH 1906.11.30.50, Cezimbru, Portugal, spirit specimen.

BMNH 1960.8.18.39-41, Ascension Island, cleared and stained specimen.

†BLOCHIUS

B. longirostris

BMNH 19940 & P4142 (2 counterparts), Monte Bolca, nr Verona, Italy, Lutetian (Monte Bolca Formation).

BMNH P4141, Monte Bolca, nr Verona, Italy, Lutetian (Monte Bolca Formation).

USNM 2695329, Verona, Monte Bolca, Italy, Lutetian (Monte Bolca Formation).

B. **sp.**

USNM 2313, near Estabanat, SE Iran, Tertiary Oligocene?

†CASIERICHTHYS

C. morsensis

BMNH 23994 and 23995, **Holotype**, Skarrehage Pit, Island of Mors, Denmark, Ypresian (Mo-Clay).

CORYPHAENA

C. equiselis

BMNH 1870.11.30.13, no data, larvae.

C. hippurus

BMNH uncat (contains label with "112"), spirit specimen (x-rayed).

BMNH uncat., Recent skeleton

BMNH 1866.8.14.199, no data, spirit specimen (x-rayed).

BMNH 1901.3.5.90, no data, Recent skull

BMNH 1931.12.5.372, Plymouth Bay, Trinidad & Tobago, spirit specimen.

BMNH 1986.7.10.11-12, off South Africa, cleared and stained specimen.

†CYLINDRACANTHUS

C. gigas

BMNH 893-5 (**Holotype**), rock of the Great Sphinx, Egypt, Eocene.

C. rectus

BMNH 25859 (supposed **Syntype**), Bracklesham Bay, Sussex, England, Ypresian-Lutetian (Bracklesham Beds).

BMNH 38881, Sheppey, England, Ypresian (London Clay).

BMNH 38881a, Sheppey, England, Ypresian (London Clay).

BMNH P11845-8, Ameki, Ombialla District, Nigeria, Lutetian.

BMNH P4304, Barton Cliff, Hampshire, England, Bartonian (Barton Clay).

BMNH P6232, Sheppey, England, Ypresian (London Clay).

C. **sp.**

BMNH P48574, Damascus, Syria, Upper Cretaceous

DICROTUS **(mostly labelled as *Promethicthys*)**

†*D. maicopicus*

PIN 848-131, **Holotype**, Kurdzhips River, Russia, Upper Oligocene?: Chattian (Zuramakent Horizon).

D. prometheus

BMNH no collection number, No data, Recent skeleton.

BMNH uncat (mentioned as *Dicrotus armatus* in Günther's BMNH catalog, 1860, Vol. 2: 349), no data, larva.

BMNH 1859.5.28.51 (labelled as "*Thyrsites prometheus*"), Madeira, Portugal, spirit specimen (x-rayed).

BMNH 1861.6.4.1 (labelled as "*Dicrotus armatus*"), no data.

BMNH 1953.12.31.5 (**Holotype** of *Dicrotus armatus*), no data, larva.

BMNH 1989.9.25.38, off Egg Island, St. Helena Islands, spirit specimen.

USNM 174935, Tokyo Market, Japan, Recent skeleton.

USNM 174934, Tokyo Market, Japan, Recent skeleton.

†DUPLEXDENS

D. macropomus

BMNH 28755, **Holotype** of *Scombramphodon sheppeyensis*, Sheppey, England, Ypresian (London Clay).

BMNH 28758 (labelled as *Scombramphodon sheppeyensis*), Sheppey, England, Ypresian (London Clay).

BMNH 38907 (labelled as *Scombramphodon crassidens*), Sheppey, England, Ypresian (London Clay).

BMNH P158 (labelled as *Sphyraenodus crassidens*), Sheppey, England, Ypresian (London Clay).

BMNH P166 (labelled as *Scombrinus macropomus*), Sheppey, England, Ypresian (London Clay).

BMNH P12954 (**Holotype** of *Acestrus elongatus*), Sheppey, England, Ypresian (London Clay).

BMNH P4145 (labelled as *Scombrinus macropomus*), Sheppey, England, Ypresian (London Clay).

GLAHM V2017 (labelled as unidentified scombroid), England, Ypresian (London Clay).

GLAHM V3470 (labelled *Scombrinus macropomus*), Sheppey, England, Ypresian (London Clay).

†aff. DUPLEXDENS

BMNH 38903 (stored as "Scombroid"), Sheppey, England, Ypresian (London Clay).

†ENNISKILLENUS

E. radiatus

BMNH 33136 (**Paratype**), Sheppey, England, Ypresian (London Clay).

BMNH P646 (**Holotype**), Sheppey, England, Ypresian (London Clay).

BMNH P1741 (**Paratype**), Sheppey, England, Ypresian (London Clay).

BMNH P26893 (**Paratype**), Sheppey, England, Ypresian (London Clay).

†EOCOELOPOMA

E. colei

BMNH P623a (**Holotype**), Sheppey, England, Ypresian (London Clay).

BMNH P12945 (labelled as *Scombrinus macropomus*), Southend-on-Sea, Essex, England, Ypresian (London Clay).

BMNH P26702 (labelled as *Eocoelopom curvatum*), Sheppey, England, Ypresian (London Clay).

BMNH P26805 (labelled as *Scombrinus*), Sheppey, England, Ypresian (London Clay).

USNM 22388 (labelled as*Scombrinus macropomus*), Sheppey, England, skull, Ypresian (London Clay).

E. curvatum

BMNH 24613, Sheppey, England, Ypresian (London Clay).

BMNH 40204, **Paratype** of *Scombrinus nuchalis*, Sheppey, England, Ypresian (London Clay).

BMNH P4151, Sheppey, England, Ypresian (London Clay).

BMNH P9455, Sheppey, England, Ypresian (London Clay).

BMNH P9456a (**Paratype** of *Scombrinus nuchalis*), Sheppey, England, Ypresian (London Clay).

BMNH P26714 (stored as "*E. gigas*"), Sheppey, England, Ypresian (London Clay).

USNM 22389 (labelled as *Scombrinus macropomus*), Sheppey, England, skull, Ypresian (London Clay).

E. gigas

BMNH 33305 (labelled as "*E. colei*"), Sheppey, England, Ypresian (London Clay).

E. portentosa

PIN 1762-85, **Holotype**, Uilya-Kushlyuk village, Turkmenistan, Ypresian, (Middle Danatinsk Svita.

E. **sp.**

BMNH P26706 (labelled as *Eocoelopoma curvatum*), Sheppey, England, Ypresian (London Clay).

BMNH P29983, Bognor Regis, Sussex, England, Ypresian (Lower Fish Tooth Bed, London Clay).

†EOTHYNNUS

E. salmoneus

BMNH 28757, Sheppey, England, Ypresian (London Clay).

BMNH P26899, Sheppey, England, Ypresian (London Clay).

EPINNULA

E. magistralis

USNM 110009, Cuba, Recent skeleton

EUPLEUROGRAMMUS

E. glossodon

BMNH uncat. (labelled as *Eupleurogrammus muticus*), no data (x-rayed).

EUTHYNNUS

E. affinis

USNM 269025, Zanzibar, Indian Ocean, Recent skeleton.

E. alletteratus

BMNH 1889.7.20.61 (labelled as *Thunnus thunnina*), Japan, larva.

BMNH 1921.7.28.25, Tobago, spirit specimen.

BMNH 1935.3.5.50-1, Haifa, Israel, two spirit specimens (one of which x-rayed).

USNM 25852 (formerly Bone Cat. 1), Received from Army Medical Museum, Recent skeleton.

†EUTRICHIURIDES

E. winkleri

BMNH P21321-9 (labelled as "*Eutrichiurides*"), Warden Point, Sheppey, England, Ypresian (London Clay).

BMNH P26097-107, Sheppey, England, Ypresian (London Clay).

BMNH P26904, Sheppey, England, Ypresian (London Clay).

BMNH P49757, Abbey Wood, England, Thanetian: Upper Palaeocene (Oldhaven/Blackheath Beds).

BMNH P65194, South England, Bartonian (Upper Barton beds).

GASTEROCHISMA

G. melampus

BMNH 1886.11.18.34, Purakanui, Otago, New Zealand, spirit specimen (x-rayed).

USNM 270404, Uruguay, Recent skeleton.

USNM 270405, Shoyu Maru, Pacific, Recent skeleton.

USNM 270406, possibly Miami, U.S.A., Recent skeleton.

USNM 270408, 20°S, 60°E, Indian Ocean, Recent skeleton.

USNM 270409, Indian Ocean, Recent skeleton.

USNM 270414, no data, Recent dorsal bones.

USNM 343334, (labelled "*Gasterochisma*"), no data, Recent skeleton.

†GEMPYLINAE/TRICHIURINAE INDET.

BMNH P10687 (labelled as *Lepidopus*), Delatyn, Galicia, Spain, Oligocene.

GEMPYLUS

G. serpens

BMNH 1952.11.27.1, Discovery expedition, larva.

BMNH 1998.2.12.12, Discovery expedition, spirit specimen (x-rayed).

USNM 26919, Cuba?, Recent skeleton.

USNM 26920, Cuba?, Recent skeleton.

†GEN ET SP. NOV.

PIN uncat., **Large**, river Belaya (coll. Bannikov '89), Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN uncat., **Middle**, river Belaya (coll. Bannikov '91), Caucasus, Russia, Lower Oligocene: Rupelian (Khadum deposits).

PIN uncat., **Small**, river Belaya (coll. Bannikov, '90), Caucasus, Russia, Middle Oligocene (Lower Maykop deposits: Khadum/Miatly-Mutsidakal Horizon).

†GIGANTOTHAZARD

G. aurorensis

USNM 319668, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., dentary, Early Pliocene: Zanclean (Yorktown Formation).

USNM 498666, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., tooth, Early Pliocene: Zanclean (Yorktown Formation).

USNM 498665, South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., jaw fragment, Early Pliocene: Zanclean (Yorktown Formation).

USNM 498670, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Early Pliocene: Zanclean (Yorktown Formation).

†aff GIGANTOTHAZARD

USNM 498675, no data, fossil hypural plate

†GODSILLA

G. lanceolata

BMNH P3946 (labelled as "*Thynnus lanceolatus*"), Monte Bolca, N. Italy, Lutetian (Monte Bolca Formation).

GRAMMATORCYNUS

G. bicarinatus

BMNH 1872.4.6.25, N. Celebes, Indonesia, spirit specimen (x-rayed).

G. sp.

BMNH uncat. (labelled "Scombridae indet.), Aden, Recent skull among non-*Grammatorcynus* bones.

GYMNOSARDA

†G. prisca

BMNH P6485 (labelled as "unidentified teleost"), **Holotype**, Sheppey, England, Ypresian (London Clay).

PIN 1878-4 (labelled as *Scomberomorus saevus*), Mangyshlak peninsula, Kazakhstan, Upper Eocene: Priabonian (Shorym Svita).

G. unicolor

BMNH 1934.3.31, Red Sea, spirit specimen (x-rayed).

†G. sp.

BMNH P1773b, (labelled"Scomberoides"), Sheppey, England, Ypresian (London Clay)

BMNH P7537 (in part), Malta, Lower Miocene (Burdigalian-Landinian, vertebrate beds of *Globigerina* Limestone).

†cf. GYMNOSARDA

cf. Gymnosarda sp.

BMNH 40278 (a) (labelled as *Xiphiorhynchus*), Brooks, Brooks, Hampshire, England, Thanetian-Ypresian (Reading and Woolwich Formations)

BMNH P4546, Sheppey, England, Ypresian (London Clay).

†HEMIRHABDORHYNCHUS

H. elliotti

BMNH P21304 (Holotype), Sheppey, England, Ypresian (London Clay).

†HOMORHYNCHUS

H. colei

PIN 1413-5, river Belaya, Caucasus, Russia, Lower Oligocene: Rupelian (Khadum deposits).

PIN 3363-134, river Belaya, North Caucasus, Russia, Lower Oligocene: Rupelian.

PIN 3363-135, river Belaya, North Caucasus, Russia, Lower Oligocene: Rupelian.

†ISTIOPHORIDAE INDET.

BMNH P13713-7 (labelled *Cylindracanthus rectus*), Ameki, Ombialla District, Nigeria (Lutetian).

BMNH P21306 (**Holotype** of *Xiphiorhynchus parvus*), Sheppey, England, Ypresian (London Clay).

USNM 244484 (labelled as *Makaira homalorhamphus*), South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., rostrums, Early Pliocene: Zanclean (Yorktown Formation).

USNM 353510, 6.4 km by road W of Post Office at a few hundreds of meters N of State Route 41, immediately W of Tuckahoe Church, Jones Co, North Carolina, U.S.A., Eocene? (Claibornain Castle Hayne Formation).

USNM 498678 & 498681-498683, rostrums (formerly lumped together in "Lot 21"), Aurora, Lee Creek Mine, North Carolina, U.S.A., Miocene (Fish Stratigraphic Column, Pungo River Formation).

ISTIOPHORUS

I. platyperus

USNM 102049, (labelled as *Istiophorus orientalis*), Cocos Island, Pacific, Recent skeleton.

I. **sp.**

BMNH 1873.4.3.220, 30° 30'N-30°, 10' O/W, larva.

BMNH 1960.8.18.3, no data, juvenile spirit specimen.

BMNH uncat., no data, Recent skeleton.

USNM 110039, (mixed with Gempylid bones in the same sample), no data, Recent skeleton.

USNM 110040, no data, Recent skeleton.

USNM 270982 (formerly USNM Bone 26341), no data, Recent skeleton.

KATSUWONUS

K. pelamis

BMNH 1893.9.26.2, Luce Bay, Scotland, spirit specimen.

BMNH 1946.5.23.15, St. Helena, spirit specimen (x-rayed).

LEPIDOCYBIUM

L. flavobrunneum

BMNH 1953.11.1.229, Funchal Market, Madeira, Portugal, spirit specimen.

USNM 343331, Atlantic, Recent skeleton.

USNM 343332, probably Oregon Station, Recent skeleton.

USNM 343333 (labelled "*Lepidocybium*"), no data, Recent skeleton.

LEPIDOPUS

L. caudatus

BMNH, no data, Recent skeleton.

BMNH 1903.6.27.22, Azores, spirit specimen (x-rayed).

LEPTURACANTHUS

L. savala

BMNH 1984.1.12.30-33, Penang Batu Maney, Singapore, spirit specimens (one of which x-rayed)

LIZA

L. tade

BMNH 1889.2.1.3698-9, spirit specimens, one of which cleared and stained.

LUVARUS

L. imperialis

BMNH 1866.5.28.24, no data, spirit specimen (x-rayed).

BMNH 1921.10.15.1, outside of Straits of Gibraltar, larva.

MAKAIRA

M. nigricans

USNM 196019, North Carolina, U.S.A., Atlantic, 36°07'N, 73°25'W, Recent skeleton and cast.

M. sp.

†BMNH P21086-8, Alum Bay, Isle of Wight, Bartonian (Lower Barton Clay).

†BMNH 30798, Sheppey, England, Ypresian (London Clay).

BMNH uncat., Recent skull.

†MAKAIROIDES

M. melitensis

BMNH P6206 (labelled "*Cybium*"), **Holotype**, Malta, (Burdigalian-Landinian, vertebrate beds of *Globigerina* Limestone).

†MICRORNATUS

M. hopwoodi

BMNH 36136, **Holotype** of *Eocoelopoma hopwoodi*, Sheppey, England, Ypresian (London Clay).

MUGIL

M. cephalus

BMNH 1913.12.9.191-2 (labelled as *Valamugil perusii*), Miniha R., Papua New Guinea, cleared and stained specimen.

NEALOTUS

N. tripes

BMNH 1887.12.7.12, N. Atlantic, larva.

BMNH 1926.6.30.484, no data, two spirit specimens (one of which x-rayed).

BMNH 1988.8.9.12737-8 (labelled as *Nesiarchus nasutus*), no data , spirit specimen.

NEOEPINNULA

N. orientalis

BMNH 1986.9.8.164-5, Lombok, Indonesia, two spirit specimens (one of which x-rayed).

BMNH 1986.9.8.1155, Jetindo Fish Trawl Survey of Indonesia, cleared and stained specimen.

NESIARCHUS

N. nasutus

BMNH 1867.7.23.5, Portugal, spirit specimen (x-rayed).

†PALAEOCYBIUM

P. proosti

BMNH 36166 (labelled as *cf. Cybium proosti*), Sheppey, England, Ypresian (London Clay).

†PALAEORHYNCHUS

"P. crios"

PIN 1413-79, **Holotype**, Tbilisi, Georgia, Middle Eocene (Dabakhansk Svita).

P. glarisianus

BMNH 41815, Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers)

BMNH 41818, Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers)

BMNH P15511, Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers)

BMNH P1714, Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers)

P. parini

PIN 4425-13, **Holotype**, river Pshekha, left bank, 1 km above Gornyy Luch village, Caucasus, Russia, Middle Eocene (Bartonian, Kuma Horizon).

PIN 4425-14, **Paratype**, river Pshekha, left bank, 1 km above Gornyy Luch village, Caucasus, Russia, Middle Eocene (Bartonian, Kuma Horizon).

PIN 4425-15, river Pshekha, left bank, 1 km above Gornyy Luch village, Caucasus, Russia, Middle Eocene (Bartonian, Kuma Horizon).

PIN 4425-16, river Pshekha, left bank, 1 km above Gornyy Luch village, Caucasus, Russia, Middle Eocene (Bartonian, Kuma Horizon).

P. senectus

PIN 1413-80, **Holotype**, Tbilisi, Georgia, Middle Eocene (Dabakhansk Svita).

P. zittelli

PIN 1413-49, river Belaya, Caucasus, Russia, Lower Oligocene: Rupelian (Upper/Middle Khadum deposits).

†*PALAEOTHUNNUS*

P. parvidentatus

PIN 1762-86, Uilya-Kushlyuk village, Turkmenistan, Ypresian (Middle Danatinsk[8]) Svita).

PIN 3363-20, **Holotype**, Uilya-Kushlyuk village, Turkmenistan, Ypresian (Middle Danatinsk Svita).

PIN 3363-21, **Paratype**, Uilya-Kushlyuk village, Turkmenistan, Ypresian (Middle Danatinsk Svita).

PIN 3363-22, **Paratype**, Uilya-Kushlyuk village, Turkmenistan, Ypresian (Middle Danatinsk Svita).

†*PALIMPHYES*

P. chadumicus

PIN 290-3, **Holotype**, North Osetiya, Russia, Lower Oligocene: Rupelian (Khadum deposits).

PIN 290-8, **Paratype**, North Osetiya, Russia, Lower Oligocene: Rupelian (Khadum deposits).

PIN 3363-136, river Belaya, North Caucasus, Russia, Lower Oligocene: Rupelian.

PIN 3363-137, river Belaya, North Caucasus, Russia, Lower Oligocene: Rupelian.

P. elongatus

BMNH 41821, Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

BMNH uncat., Engi, Canton Glarus, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

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[8] Danil'chenko (1968) assumed that the fish beds from the Danatinsk Svita were from the Lower Danatinsk and thus Upper Palaeocene. It was shown that these fish beds are of the Middle Danatinsk, which is Ypresian (Tyler & Bannikov, 1992; Harland *et al.*, 1990)

P. cf. elongatus

BMNH P4952, Plattenberg, Switzerland, Lower Oligocene: Rupelian (Glarnerschiefers).

P. palaeoceanicus

PIN 2179-83, **Holotype**, Uilya-Kushlyuk village, Turkmenistan, Ypresian, (Middle Danatinsk Svita).

P. pinnatus

PIN 1413-77, **Holotype**, Tbilisi, Georgia, Middle Eocene (Dabakhansk Svita).

P. pshekhaensis

PIN 4425-7, **Paratype**, Krasnodar territory, river Pshekha, 1 km upstream from Gornyy Luch Farm, Caucasus, Russia, Bartonian (Kuma horizon).

PIN 4425-12, **Holotype**, Krasnodar territory, river Pshekha, 1 km upstream from Gornyy Luch Farm, Caucasus, Russia, Bartonian (Kuma horizon).

†*PROGEMPYLUS*

P. edwardsi

BMNH 32388, **Holotype**, Sheppey, England, Ypresian (London Clay).

†*PSEUDOTETRAPTURUS*

P. luteus

PIN 1413-50, **Holotype**, river Sulak, Caucasus, Russia, Upper Eocene: Priabonian (Riki Horizon).

PIN 1413-51, **Paratype**, river Sulak, Caucasus, Russia, Upper Eocene: Priabonian (Riki Horizon).

RASTRELLIGER

R. kanagurta

BMNH 1871.7.15.28, Red Sea, spirit specimen (x-rayed).

REXEA

R. antifurcata

BMNH 1997.5.21.40, Norfolk Ridge, S.W. Pacific, spirit specimen (x-rayed).

R. promethoides

BMNH 1986.9.8.150, off South coast of East Java and Bali, Indonesia.

†*R. sp.*

BMNH P37337 (stored as ~~*Hemithyrsites*~~ *Acanthonothus*), Asmari Mountain, Masjid-i-Sulaiman, Iran, Eocene?

†*ROTUNDORHYNCHUS*

R. brittannicus

BMNH P23838, Sheppey, England, Ypresian (London Clay).

BMNH P1765, **Holotype**, Sheppey, England, Ypresian (London Clay).

RUVETTUS

R. pretiosus

BMNH 1909, No data, Recent skeleton.

BMNH 1938.6.23.24, off Chonsi, Japan, spirit specimen (x-rayed).

USNM 51394, Hawaii, Recent skeleton.

USNM 344426 (formerly Bone cat. 26092, labelled as *Ruvettus temmincki*), no data, Recent skeleton.

SARDA

†*S. delheidi*

USNM 265382, Popes Creek, Bluff 1 mile S of, 1 ft above beach and 15 ft below gray Carbonaceous clay bed, Charles Co, Maryland, U.S.A., Ypresian (Pamunkey Group, Nanjemoy Formation).

†*S. memorabilis*

PIN 3363-91, **Holotype**, Caucasus, Azerbaijan, Upper Oligocene: Chattian (Zuramakent Horizon).

PIN 3363-92, Urup River, Otradnaya village, Caucasus, Sakaraul'skii regional yarus, Russia, Lower Miocene (Karadzhalgin Svita).

PIN 1413-99, North Osetiya, river Chyorna[9], Russia, Lower Miocene (Assinskaya Svita).

S. orientalis

BMNH 1920.7.23.59, Durban, South Africa, spirit specimen (x-rayed).

†*S. rara*

PIN 483-2, originally catalogued as *Thunnus abchasicus*, North Osetiya, Russia, Lower Oligocene: Rupelian (Lower Khadum Horizon).

PIN 3363-18, **Holotype**, river Belaya in Abadzekhskaya village, Caucasus, Russia, Lower Oligocene (Pshekha Svita).

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9 Chyornaya rechka, here translated river Chyorna, literally means "Black river".

†*S. remota*

PIN 1413-34 (catalogued as *Scomber voitestii*), river Gumista, Abkhazia, Georgia, Middle Oligocene (Miatly-Mutsidakal Horizon).

PIN 1413-45, **Holotype**, river Belaya, Russia, Caucasus, Upper Oligocene: Chattian (Morozkina Ravine Horizon).

S. sarda

USNM 26953 (formerly Bone Cat. 1, labelled as *Scomberomorus*), no data, Recent skeleton.

USNM 26954 (formerly Bone Cat. 1, labelled as *Scomberomorus*), no data, Recent skeleton.

USNM 109997 (formerly Mam. Cat 11939), Woods Hole, Massachusetts, U.S.A., Pacific, Recent skull.

†USNM 476225, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Early Pliocene: Zanclean (Yorktown Formation).

USNM 270730, New Jersey, U.S.A., Atlantic, Recent skeleton.

USNM 270731, Ponte Delgada Fish Market, San Miguel, Azores, Atlantic, Recent skeleton.

†*S. aff. sarda*

USNM 290544 (see also Pudy *et al.*, 2000), South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., skull portion, Early Pliocene: Zanclean (Yorktown Formation).

†*S. sp.*

PIN 1878-6, Mangyshlak peninsula, Kazakhstan, Upper Eocene: Priabonian (Shorym Svita).

PIN 1878-7, Mangyshlak peninsula, Kazakhstan, Upper Eocene: Priabonian (Shorym Svita).

several (un)cataloged USNM specimens (under which no. 289356, ethmoidal region), South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Early Pliocene: Zanclean (Yorktown Formation).

USNM 289329, South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Early Pliocene: Zanclean (Yorktown Formation).

USNM 476369 (see also Purdy *et al.*, 2000), South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Miocene (Fish Stratigraphic Column, Pungo River Formation).

USNM 476396, South side of Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Early Pliocene: Zanclean (Yorktown Formation).

†**SARDINI INDET.**

BMNH P9459 (labelled as *Eocoelopoma colei*), Sheppey, England, Ypresian (London Clay).

†*cf.* **SARDINI**

BMNH P45150 (labelled as *Eocoelopoma colei*), Sheppey, England, Ypresian (London Clay).

SCOMBER

S. australasicus

BMNH 1873.12.13.13, New Zealand, juvenile spirit specimen (x-rayed).

USNM 343318, Sydney Fish Market, Australia, Pacific, Recent skeleton.

USNM 343319, Sydney Fish Market, Australia, Pacific, Recent skeleton.

†*S. cubanicus*

PIN 484-11, **Holotype**, Khadyzhenskaya Cossack village, Krasnodar territory, Caucasus, Russia, Upper Oligocene: Chattian (Riki Horizon).

PIN 2180-11, Pirekishkyul' village, Azerbaijan, Upper Oligocene (Abadzekh Horizon).

†*S. gnarus*

PIN 485-24, North Osetiya, river Chyorna, Russia, Lower Miocene (Assin Svita).

PIN 1434-34, river Pshekha in Shirvanskaya village, North Azerbaijan, Upper Oligocene: Chattian (Zuramakent Horizon).

PIN 2180-9, Pirekishkyul' village, Azerbaijan, Lower Miocene (Sulak Svita).

PIN 2180-10, Pirekishkyul' village, Azerbaijan, Lower Miocene (Sulak Svita).

PIN 3363-27, **Holotype**, river Pshekha in Shirvanskaya village, North Azerbaijan, Upper Oligocene: Chattian (Voskovorskiy Horizon).

PIN 3363-36, river Pshekha, in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

PIN 3363-38, river Pshekha in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

PIN 3363-40, river Pshekha, in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

PIN 3363-41, river Pshekha in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

PIN 3363-43, river Pshekha, in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

PIN 3363-44, river Pshekha, in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

PIN 3363-45, river Pshekha, in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

PIN 3363-46, river Pshekha, in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

PIN 3363-47, river Pshekha, in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

PIN 3363-48, river Pshekha, in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

PIN 3363-50, river Pshekha, in Shirvanskaya village, Azerbaijan, Lower Miocene (Voskovogor Svita).

S. japonicus

USNM 260648, Tokyo Market, Japan, Pacific, Recent skeleton.

S. scombrus

USNM 269008 (orig. No. 59, formerly Bone Cat. 26278), North Atlantic, Recent skeleton.

KAM 4 ("Curly"), purchased from fishmonger, Bristol, 1996.

KAM 5 ("Larry"), purchased from fishmonger, Bristol, 1996.

KAM 6 ("Moe"), purchased from fishmonger, Bristol, 1996.

†S. voitestii

PIN 491-10, North Pasechnaya, Predcarpathians, Ukraine, Lower Oligocene: Rupelian (Menilite Svita).

PIN 491-11, North Pasechnaya, Predcarpathians, Ukraine, Lower Oligocene: Rupelian (Menilite Svita).

S. sp.

BMNH uncat. (labelled as *Rastrelliger*), coll. in Zanzibar, 1965, cleared and stained specimen.

†SCOMBER?

PIN uncatalogued "*Scomber gnarus*", very large specimen.

***†SCOMBERODON/NEOCYBIUM* sp.**

BMNH P14029 (one of), Barton, Hampshire, England, Bartonian (Barton Clay). Some items catalogued under this number are described under *Scomberomorus excelsus* and *Acanthocybium.*

BMNH 38883 (labelled *Xiphiorhynchus*), **Holotype**, Sheppey, England, Ypresian (London Clay).

BMNH 19888, Abbey Wood, England, Thanetian: Upper Palaeocene (Blackheath Beds).

BMNH 25710 (in part, labelled "scombroid"), no data.

BMNH P27002, Sheppey, England, Ypresian (London Clay).

BMNH 241686c (labelled as "not istiophorid"), Sheppey, England, Ypresian (London Clay).

USNM 286186 (labelled Xiphiorhynchus?), Lee Creek Mine, South side of Pamlico River, Aurora, Beaufort Co., North Carolina, U.S.A., Early Pliocene: Zanclean (Chesapeake Group, Yorktown Formation).

USNM 498664, Lee Creek Mine, South side of Pamlico River, Aurora, Beaufort Co., North Carolina, U.S.A., Early Pliocene: Zanclean (Chesapeake Group, Yorktown Formation).

USNM 498677 (formerly in box with *Acanthocybium*, labelled Scombridae), no data, probably South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., hypural plate, Early Pliocene: Zanclean (Yorktown Formation).

USNM 498672, Lee Creek Mine, South side of Pamlico River, Aurora, Beaufort Co., North Carolina, U.S.A., Early Pliocene: Zanclean (Chesapeake Group, Yorktown Formation).

PIN 1878-5, Mangyshlak peninsula, Kazakhstan, Upper Eocene: Priabonian (Shorym Svita).

†SCOMBEROMORINAE INDET.

BMNH P1530, Isle of Wight, Lutetian (Bracklesham Beds).

BMNH P27896-27899 (labelled "*Cybium*"), Southampton, England, Ypresian-Lutetian (Bracklesham Beds).

BMNH P42683-5, (labelled *Cybium? proosti*), Lower Fish-tooth bed, Bognor Regis, England, Ypresian (London Clay).

SCOMBEROMORUS

†S. avitus

PIN 1762-86, **Holotype**, Uilya-Kushlyuk village, Turkmenistan, Lower Eocene (Ypresian, Middle Danatinsk Svita).

PIN 1762-87, **Paratype**, Uilya-Kushlyuk village, Turkmenistan, Lower Eocene (Ypresian, Middle Danatinsk Svita).

S. brasiliensis

USNM 269660 (see also Collette & Russo, 1984)French Guyana, Pacific, Recent.

USNM 269669 (see also Collette & Russo, 1984), Santos, Southwest Brazil, Atlantic, Recent.

USNM 26699670 (see Collette & Russo, 1984)Brazil, Atlantic, Recent.

S. cavalla

USNM 110012 (Mam. Cat. 11676), off the U.S.A. coast, Atlantic, see also Collette & Russo, 1984), Recent skeleton.

USNM 269662 (see aslo Collette & Russo, 1984), off Miami, Florida, U.S.A., Atlantic, Recent skeleton.

USNM 269671 (see also Collette & Russo, 1984), Western Atlantic, probably Florida (U.S.A.), Recent skeleton.

S. commerson

BMNH 1984.1.12.34-36, Penang Bath Maney, Singapore Fisheries Research Station, cleared and stained specimens.

USNM 111197, New Caledonia, South Pacific, Recent skeleton.USNM 269664 (see also Collette & Russo, 1984), Fish Market, Philippines, Pacific, Recent skeleton.

USNM 269665 (see also Collette & Russo, 1984), Koki Market, Papua New Guinea, Pacific, Recent skeleton.

USNM 269667 (see also Collette & Russo, 1984), West Wharf Market, Karachi, Pakistan, Indian Ocean, Recent.

USNM 269673 (see also Collette &Russo, 1984), Cotts Harbor, New South Wales, Australia, Pacific, Recent.

USNM 269674 (see also Collette &Russo, 1984)Cotts Harbor, New South Wales, Australia, Pacific, Recent.

S. concolor

USNM 269677 (see also Collette & Russo, 1984),Mexico, Gulf of California, Recent skeleton.

USNM 269678 (see also Collette & Russo, 1984), Mexico, Gulf of California, Recent skeleton.

USNM 269680 (see also Collette & Russo, 1984), Mexico, Gulf of California, Recent skeleton.

USNM 269682 (see also Collette & Russo, 1984), Mexico, Gulf of California, Recent skeleton.

†***"S. excelsus"***

BMNH 1193 (labelled as "*Cybium bartonensis*"), Barton, England, Bartonian (lower Barton Clay).

BMNH P14029 (discarticulated skeleton), Barton, England, Bartonian (Barton Clay). Some material of this number is mentioned under *Acanthocybium* and *Scomberodon.*

BMNH P53, **Holotype** of *Cybium bartonensis*, near Christchurch, Hampshire, England, Bartonian (lower Barton Clay).

BMNH P1528, **Holotype**, Barton Cliff, Hampshire, England, Bartonian (Barton Clay).

BMNH P3958 (labelled as "*Cybium bartenensis*"), Barton Cliff, Hampshire, England, Bartonian (Barton Clay).

S. guttatus

USNM269696, (see also Collette & Russo,1984), West Wharf Market, Karachi, Pakistan, Indian Ocean, Recent skeleton.

USNM 269705 (see also Collette & Russo, 1984), no data, Recent skeleton.

S. koreanus

USNM 269711 (see also Collette & Russo, 1984), Japan, probably Pacific, Recent skeleton.

USNM 269713 (see also Collette & Russo, 1984), Japan, probably Pacific, Recent skeleton.

USNM 269714 (see also Collette & Russo, 1984), Tokyo Market, Japan, West Pacific, Recent skeleton.

USNM 270081 (see also Collette & Russo, 1984), Indonesia, Pacific, Recent skeleton.

S. maculatus

USNM 110006 (Mam. Cat. 11476), Woods Hole, Massachusetts, U.S.A., Atlantic, Recent skeleton.

USNM 269719 (see also Collette & Russo, 1984), Washington DC Fish Market, U.S.A., Recent skeleton.

USNM 269721 (see also Collette & Russo, 1984), Washington DC Fish Market, U.S.A., Recent skeleton.

USNM 269726 (see also Collette & Russo, 1984), 36°27'N, 75°33' 40"W, SE of Chesapeake Bay, U.S.A., Recent skeleton.

USNM 269732 (see also Russo & Collette, 1984), 31°2' 12"N, 81°18' 9"W, Atlantic, Recent skeleton.

S. multiradiatus

USNM 269750 (see also Collette & Russo, 1984), Karema Bay, Papua New Guinea, Pacific, Recent skeleton.

USNM 270069 (see als Collete & Russo, 1984), Fresh Water Bay, Papua New Guinea, Pacific, Recent skeleton.

USNM 270084 (see als Collete & Russo, 1984), Fresh Water Bay, Papua New Guinea, Pacific, Recent skeleton.

S. munroi

USNM 269752, Irian Jaya, Indonesia, Pacific, Recent skeleton.

USNM 270085 (see also Collette & Russo, 1984), Irian Jaya (Indonesia) or Papua New Guinea, Pacific, Recent skeleton.

S. niphonius

BMNH 1874.1.16.9, no data, spirit specimen (x-rayed).

BMNH 1890.2.26.90, Inland Sea, Japan, spirit specimen (x-rayed).

USNM 110984, (labelled as *Cybium niphonium*), Idzu, Japan, Pacific, stuffed skin.

S. plurilineatus

USNM 264809, Addington Seine Nets, Durban, Natal, South Africa, Indian Ocean, 2 specimens: one in tank (not seen) and Recent skeleton.

USNM 269760 (see also Collette & Russo, 1984), Durban, Natal, South Africa, Indian Ocean, Recent skeleton.

S. queenslandicus

USNM 269755 (see also Collette & Russo, 1984[10]), Exmouth Gulf, W. Australia, Indian Ocean, Recent skeleton.

USNM 270087 (see also Collette & Russo, 1984), 7°56' 30"S, 144°58' 18"E, Papua New Guinea, Pacific, Recent skeleton.

USNM 289726, Pt, Lookout, S.E. Queensland, Australia, Pacific, Recent.

USNM 269756 (see also Collette & Russo, 1984),18°45'S, 146°40"E, Hayman Rk., Palm Is., Australia, Pacific, Recent Skeleton.

S. regalis

USNM 110011 (Mam. Cat. 13540), Cuba, Recent jaw bones.

USNM 270053 (see also Collette & Russo, 1984),Bahamas, Recent skeleton.

USNM 270054 (see also Collette & Russo, 1984), Bahamas, Recent skeleton.

USNM 270055 (see also Collette & Russo, 1955), 3-7 miles South of Key West, Eastern Dry Rocks, Floriida, U.S.A., Gulf of Mexico, Recent skeleton.

†*S. saevus*

PIN 1878-3, Mangyshlak peninsula, Kazakhstan, Upper Eocene: Priabonian (Shorym Svita).

PIN 1878-8 (**Holotype**), Mangyshlak Peninsula, Karagiye basin, Kazakhstan, Upper Eocene: Priabonian (Shorym Svita)

PIN 1878-9 (prootic), Mangyshlak peninsula, Karagiye basin, Kazakhstan, Upper Eocene: Priabonian (Shorym Svita).

S. semifasciatus

USNM 269765 (see also Collette & Russo, 1984), Irian Jaya (Indonesia) or New Guinea, Pacific, Recent skeleton.

USNM 270058 (see also Collette & Russo, 1984), Irian Jaya (Indonesia) or New Guinea, Pacific.

USNM 270059 (see also Collette & Russo, 1984), Recent skeleton.

USNM 270061 (see also Collette & Russo, 1984), near Lea Lea Inlet, Port Moresby, Papua New Guinea, Recent skeleton.

S. sierra

USNM 270070 (see also Collette & Russo, 1984), Panama Bay, near Pearl Islands, Panama, Pacific, Recent skeleton.

USNM 270071 (see also Collette & Russo, 1984), Baja, California, U.S.A., Pacific, Recent skeleton.

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10 In the USNM collection and the USNM on-line fish catalog, this is referred to as Collette & Russo (1985), since that was the year the paper actually came out. Notwithstanding that, according to the bibliographical data of the Fishery Bulletin, Vol. 82 (4) is a 1984 issue.

USNM 270072 (see also Collette & Russo, 1984), Panama Bay, near Pearl Islands, Panama, Pacific, Recent skeleton.

USNM 270073 (see also Collette & Russo, 1984), Panama Bay, near Pearl Islands, Panama, Pacific, Recent skeleton.

S.sinensis

USNM 269706 (see also Collette & Russo, 1984), Hong Kong, China, Pacific, Recent skeleton.

USNM 270064 (see also Collette & Russo, 1984), Tokyo Market, Japan, Recent skull.

S. tritor

USNM 270066 (see also Collette & Russo, 1984), Abidjan, Côte d'Ivoire, Gulf of Guinea, Atlantic, Recent skeleton.

USNM 270075 (see also Collette & Russo, 1984), Abidjan, Côte d'Ivoire, Gulf of Guinea, Atlantic, Recent skeleton.

USNM 270100 (see also Collette & Russo, 1984), Gulf of Guinea, Atlantic, Recent skeleton.

USNM 270248 (see also Collette & Russo, 1984), Abidjan, Côte d'Ivoire, Gulf of Guinea, Atlantic, Recent skeleton.

USNM 270249 (see also Collette & Russo, 1984), Abidjan, Côte d'Ivoire, Gulf of Guinea, Atlantic, Recent skeleton.

USNM 270250 (see also Collette & Russo, 1984), 4°47' 36"N, 4°33'W, Atlantic, Recent skeleton.

S. sp.

BMNH 1935.4.24.25, Pearl St., Panama, larva.

†BMNH P15295-6, no data.

†BMNH 25700 (labelled as "scombroid"), Sussex, Lutetian (Bracklesham Beds).

†BMNH 25710 (in part, labelled as"scombroid"), no data.

†BMNH 40278 (b) (labelled as *Xiphiorhynchus*), Brooks, Hampshire, England, Thanetian-Ypresian (Reading and Woolwich Formations).

†BMNH P3959 (labelled as "*Cybium lingulatum*"), age and locality unknown (Woodward, 1901).

†BMNH P6207, Malta, Lower Miocene (Burdigalian-Landinian, vertebrate beds of *Globigerina* Limestone).

†BMNH P59739 (labelled as "*Cybium bartonensis*"), no data.

†USNM 24726, Pope's Creek, 3.7 miles below mouth (30'W (upstream) from USNM site 23690, or about 12001 beyond swamp E of big meadows, Westmoreland Co, Maryland, U.S.A., parts of jaws, Miocene (Calvert Formation).

†*SCOMBRAMPHODON*

S. crassidens

BMNH P1763, Sheppey, England, Ypresian (London Clay).

BMNH P65644, Warden Point, Sheppey, England, Ypresian (London Clay).

†SCOMBRIDAE INDET.

BMNH 39246, Bracklesham, England, Ypresian-Lutetian (Bracklesham Beds).

†SCOMBRINI INDET.

BMNH P23969 (labelled as Scombrid?), Skarrehage Pit, Island of Mors, Denmark, Ypresian (Mo-Clay).

PIN 3363-142 (labelled as *Scombrosarda* cf. *cernegurae*), river Belaya, Caucasus, Russia, Lower Oligocene: Rupelian.

†*SCOMBRINUS*

S. cernegurae (known as *Scombrosarda*)

PIN 3363-60, river Belaya in Abadzekhskaya village, Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-65, river Belaya in Abadzekhskaya village, Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-66, river Belaya in Abadzekhskaya village, Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-69, river Belaya in Abadzekhskaya village, Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-71, river Belaya in Abadzekhskaya village, Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-73, river Belaya in Abadzekhskaya village, Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-80, river Belaya in Abadzekhskaya village, Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-82, river Belaya, in Abadzekhskaya village, Caucasus, Russia, Lower Eocene: Rupelian (Psheka Horizon).

PIN 3363-83, river Gumista, Bereg Province, Abkhazia, Georgia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-138, river Belaya, North Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-139, river Belaya, North Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-140, river Belaya, North Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

PIN 3363-141, river Belaya, North Caucasus, Russia, Lower Oligocene: Rupelian (Pshekha Horizon).

S. devius (known as *Scombrosarda*)

PIN 1413-79, **Holotype**, Tbilisi, Georgia, Middle Eocene (Dabakhansk Svita).

S. nuchalis

BMNH 38919 (**Paratype**), Sheppey, England, Ypresian (London Clay).

BMNH 43117 (**Paratype**), Sheppey, England, Ypresian (London Clay).

BMNH P4148 (**Holotype**), Sheppey, England, Ypresian (London Clay).

S. speciosus

BMNH P4136 & P1989 (2 counterparts, labelled as *Cybium speciosiun*), Monte Bolca, Verona, Italy, Lutetian (Monte Bolca Formation).

BMNH P4137 (labelled as *Auxides properygius*), Monte Bolca, Verona, Italy, Lutetian (Monte Bolca Formation)

BMNH P4480 (labelled as *Orcynus lanceolatus*), 2 counterparts, Monte Bolca, Verona, Italy, Lutetian (Monte Bolca Formation).

BMNH P9942 (labelled as *Cybiun speciosum*), Monte Bolca, Verona, Italy, Lutetian (Monte Bolca Formation)

BMNH P15091 (labelled as *Auxides propterygius*), North Italy, Lutetian (Monte Bolca Formation).

BMNH P16302 (labelled as *Auxides propterygius*, North Italy, Lutetian (Monte Bolca Formation).

BMNH P16303 (labelled as *Auxides propterygius*), North Italy, Lutetian (Monte Bolca Formation).

USNM 1946 (labelled as *Auxides propterygius*), Monte Bolca, Verona, Italy, Lutetian (Monte Bolca Formation).

S. turkmenicus (known as *Scombrosarda*)

BMNH P1898, Tangi-Kora, Imam Hassan, Iran, Middle Eocene.

PIN 2179-51, **Holotype**, Uilya-Kushlyuk village, Turkmenistan, Ypresian, (Middle Danatinsk Svita).

PIN 1762-82, Uilya-Kushlyuk village, Turkmenistan, Ypresian (Middle Danatinsk Svita).

PIN 2179-53, **Paratype**, Uilya-Kushlyuk village, Turkmenistan, Ypresian (Middle Danatinsk Svita).

SPHYRAENA

Sphyraena barracuda

BMNH 1876.5.1.26, Yukun?, spirit specimen (x-rayed).

†USNM 359506, no data, probably Miocene.

†***S.*** **aff.** ***barracuda***

USNM 28773, Lee Creek Mine, North Carolina, U.S.A., tooth (mold & cast), Early-Middle Miocene (limestone Layers, Pungo River Formation).

USNM 291076, fossil centrums, Lee Creek Formations, no data, (see also Purdy *et al.*, in press).

USNM 437516, South side of Pamlico River, near Aurora Bath, 7.5 min. Quad, Lee Creek Mine, North Carolina, U.S.A., dentary, Early Pliocene: Zanclean (Chesapeake Group, Yorktown Formation).

†***S. bolcensis***

BMNH P1781 & P3950, 2 counterparts, Monte Bolca, near Verona, Italy, Lutetian (Monte Bolca Formation).

BMNH 2139, Monte Bolca, near Verona, Italy, Lutetian (Monte Bolca Formation).

BMNH P1782, Monte Bolca, near Verona, Italy, Lutetian (Monte Bolca Formation).

BMNH 21398, Monte Bolca, near Verona, Italy, Lutetian (Monte Bolca Formation).

BMNH P3950a, Monte Bolca, near Verona, Italy, Lutetian (Monte Bolca Formation).

S. chrysotaenia

BMNH 1974.5.25.3589, Medong harbour, inside South tip of Paconai Island, cleared and stained specimen.

S. sphyraena

BMNH 1903.5.13.9 (labelled *Sphyraena picuda*), W. India, Recent skeleton.

BMNH 1908.5.28.21 (labelled *Sphyraena picuda*), Jamaica, Recent skeleton.

S. sp.

BMNH 1858.4.20.79, No data, Recent skeleton.

BMNH 1985.7.9.511, Oyster Bay, Dar-es-Salaam, Tanzania, larvae.

†BMNH P15397 (in box with 5 uncat. specimens), no data.

†USNM 402073, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., centrum, Early Pliocene Zanclean (Yorktown Formation).

†USNM406863, South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., tooth, Early Pliocene: Zanclean (Yorktown Formation).

several uncataloged USNM specimens, South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Early Pliocene: Zanclean (Yorktown Formation).

†*SPHYRAENODUS*

S. priscus

BMNH 35106 (skull), Sheppey, England, Ypresian (London Clay).

BMNH P167 (skull), Sheppey, England, Ypresian (London Clay).

BMNH P3957 (skull), **Holotype** Sheppey, England, Ypresian (London Clay)

BMNH P21669 (skull), Warden Point, Sheppey, England, Ypresian (London Clay).

BMNH P21651-54 (teeth labelled *Sphyraenodus* sp.), Sheppey, England, Ypresian (London Clay).

BMNH P25386-46 (teeth labelled *Sphyraenodus* sp.), Sheppey, England, Ypresian (London Clay).

†*STEREODUS*

S. melitensis

BMNH P6207a, Malta, Lower Miocene (Burdigaiian-Landinian, vertebrate beds of *Globigerina* Limestone).

†*TAMESICHTHYS*

T. decipiens

BMNH 41319, Sheppey, England, Ypresian (London Clay).

TENTORICEPS

T. cristatus

BMNH 1974.3.5.1-3, Singapore, spirit specimens (1974.3.5.1 x-rayed).

TETRAPTURUS

T. albidus

USNM 110013, no data, Recent skeleton.

USNM 270766, W.N. Atlantic, Recent skeleton.

USNM 270767, no data, Recent skeleton.

USNM 270268, no data, W.N. Atlantic, Recent skeleton.

USNM 270770 (formerly USNM Bone 26071), Woods Hole, Massachusetts, U.S.A., Atlantic, dried head.

T. audax

USNM 2700773, Pacific, 8°49'S, 83°33'W, Recent skeleton.

USNM 2700774, Pacific, 32°42'S, 83°48'W, Recent skeleton.

T.pfluegeri

USNM 270225, West Atlantic, Recent skeleton.

USNM 273241, no data, Recent skeleton.

†T. rotundus

BMNH P8799, Cooper River, Charleston, South Carolina, U.S.A., Tertiary (Tertiary Phosphate Beds).

***T.* sp.**

USNM 270772, Atlantic, 29°29'N, 80°19'W, Recent skeleton.

USNM 316702, no data, Recent skeleton.

†THUNNINI INDET.

BMNH P4300 (labelled as *Eothynnus*), Sheppey, England, Ypresian (London Clay).

USNM 17881 (labelled *Euthynnus* sp.), 3.3 miles N of Hannah Lake, Yakataga District, Alaska, U.S.A., Oligocene.

PIN 3363-96 (labelled Thunnidae indet.), river Belaya in Abadzekhskaya village, Caucasus, Russia, Lower Oligocene: Rupelian, (Pshekha Horizon).

THUNNUS

T. alalunga

KAM 1 ("Brenda"), purchased from fishmonger, Bristol, England, 1997.

USNM 268764, 37°1'S, 75°19'E, Indian Ocean, Recent skeleton.

USNM 268766 (see also Gibbs & Collette, 1967), 31°0'N, 39°50'W, Atlantic, Recent skeleton.

USNM 268773 (see also Gibbs & Collette, 1967), 38°8'N, 67°33'W, Atlantic, Recent skeleton.

USNM 269009, West N. Atlantic, Recent skeleton.

USNM 270407 (see also Godsil & Byers, 1944; Gibbs & Collette, 1967), Japan, Pacific, Recent skeleton.

T. albacares

BMNH 1973.2.9.33-5, Persian Gulf, spirit specimens.

USNM 268881, 18°24'N, 67°23'W, WNW of Mayaguez Bay, Puerto Rico, Recent skeleton.

USNM 268882 (see also Godsil & Byers, 1944 and Gibbs & Collette, 1967), Vicinity of Honolulu, Hawaiian Islands, Pacific, Recent skeleton.

USNM 268883, East Central Pacific, Uncle Sam Bank, Recent skeleton.

USNM 268887 (see also Gibbs & Collette, 1967), 31°51'N, 56°1' 13"W, Atlantic, Recent partial skeleton.

USNM 269019, Grand Lake Stream, Maine, U.S.A., In divided box with 269020, Recent skull and vertebrae.

USNM 270252, (in box with skull of *Katsuwonus pelamis*), North of Mona Passage, West Atlantic, Recent skeleton.

USNM 270491(see also Gibbs & Collette, 1967) 04°11'S, 75 °0'E, Indian Ocean, Recent skeleton.

USNM 270492 (see Gibbs & Collette 1967) 17°41'S, 42°31'E, Indian Ocean, Recent skeleton.

USNM 270496, Somali Coast, Recent skeleton.

USNM 270541 (see also Gibbs & Collette, 1967), 31°59'N, 56°1'W To 31°59'N, 56°13'W, Atlantic, Recent skeleton.

USNM 343335, East Atlantic, Recent anterior half of skeleton.

T. atlanticus

USNM 269023, off Miami, Florida, U.S.A., Atlantic, Recent skeleton.

USNM 270474 (see also Gibbs & Collette, 1967), between Rosalind and Sewana Banks, Caribbean, Recent skeleton.

USNM 270476,off Miami, Florida, U.S.A., Recent skeleton.

USNM 270487 (see also Gibbs & Collette, 1967), 6°42'N, 83°12'W, Caribbean, Recent skeleton.

USNM 270490 (see also Gibbs & Collette, 1967), 18°24'N, 67°23'W, Caribbean, Recent skeleton.

T. maccoyii

USNM 269006, 32°56' 42"S, 90°23' 12"E, Indian Ocean, Recent skeleton.

USNM 270467, Chile, Recent skeleton.

USNM 270468, (see also Godsil & Holmberg, 1950; Gibbs & Collette, 1967), North coast of Tasmania, Australia, Pacific, Recent skull and vertebrae.

USNM 270469 (see also Gibbs & Collette, 1967), (with different labels as: *Thunnus thynnus maccoyii*, *Thunnus thynnus* and *Thunnus maccoyii*), Sidney Market, Australia, Recent skeleton.

USNM 343316, Bermagui, New South Wales, Australia, Pacific, Recent skeleton.

T. obesus

USNM 187682, 31°8.8'S, 75°14.3'E, Recent skeleton.

USNM 187683, Christmas Island, Recent skeleton.

USNM 268890 (see also Gibbs & Collette, 1967), 30°32'N, 28°2'W, Recent skeleton.

USNM 269656 (see also Gibbs & Collette, 1967), 41°10'N, 29°10'W, West Atlantic, Recent skeleton.

USNM 269657 (see also Gibbs & Collette, 1967), 40°00'N, 049°45'W, W. Atlantic, Recent skeleton.

USNM 270417 (see also Gibbs & Collette, 1967), Western Atlantic, Recent skeleton.

USNM 270418 (see also Gibbs & Collette, 1967), no data, Recent skeleton.

USNM 270420 (see also Gibbs and Collette, 1967), 26°00'S, 54°52'E, Indian Ocean, Recent skeleton.

T. tonggol

USNM 22195, (labelled as *Thynnus macropterus*), Sagami, Kadzusa, Japan, Atlantic, dried specimen.

USNM 26894, no data, Recent skeleton.

USNM 268949, New South Wales, Australia, Pacfic, Recent skeleton.

USNM 268951, North Arabian Sea, Recent skeleton.

USNM 268952, Pakistan, Indian Ocean, Recent skeleton.

USNM 268953, (previously stored with *Thunnus obesus*), Sidney Market, New South Wales, Australia, Pacific, Recent skeleton.

T. thynnus orientalis

USNM 187563-A, rec. from California Bureau of Marine Fisheries, Recent skeleton.

USNM 268959 (see also Godsil & Beyers, 1944 and Gibbs & Collette, 1967), Guadalupe Is., Lower California (U.S.A./Mexico), Recent skeleton.

USNM 268978, California, U.S.A., Recent skeleton.

USNM 269002, Neighbouring areas of NE Japan, Paciific, Recent skeleton.

USNM 269018, Aleojos Rocks, probably Guadalupe Is. or Cataline Is., E. Pacific, Recent skeleton.

T. thynnus thynnus

USNM 29010 (see also Godsil & Holmberg, 1950 and Gibbs & Collette, 1967), Provincetown, Rhode Island, U.S.A., Atlantic, Recent skeleton.

USNM 268973, W. Atlantic, Recent skeleton.

USNM 269007 (formerly USNM 12057), Minimshi., Massachusetts, Atlantic, Recent skeleton.

USNM 269012 (see also Godsil & Holmberg, 1950 and Gibbs & Collette, 1967), Provincetown, Rhode Island, U.S.A., Atlantic, Recent skeleton.

USNM 269013 (see also Godsil & Holmberg, 1950 and Gibbs & Collette, 1967), Provincetown, Rhode Island, U.S.A., Atlantic, Recent skeleton.

USNM 269021, W. Atlantic, Recent skeleton.

USNM 269650, W. Atlantic, Recent skeleton.

†*T. sp.*

BMNH 41989 (labelled as *Thynnus thynnus*), Lea Vally, near Tottenham, England, Middle Pleistocene (Pebble Gravel).

BMNH P5583 (labelled as *Thynnus scaldisiensis*), Suffolk, Piacenzian (Red Crag).

BMNH P8737 (labelled as *Thynnus thynnus*), East Runton, Norfolk, England, Early Pleistocene (Lower Forest Bed Formation).

BMNH P9453 (labelled as *Thynnus scaldisiensis*), Aldborough, Suffolk, England, Piacenzian (Coralline Crag).

†THYRSION

T. kriegeri

USNM 10283 (labelled as *Thyrsocles kriegeri*), Lompoc, California, U.S.A., Miocene Diatomaceous beds.

USNM 10963 (labelled as *Thyrsocles velox*), Upper Miocene (Puente Formation).

USNM 11059 (labelled as *Thyrsocles velox*), Lompoc, California, U.S.A., Miocene Diatomaceous beds.

THYRSITES

T. atun

BMNH 1873.7.3.6-8, no data, three spirit specimens (one of which x-rayed).

BMNH 1916.3.20.143-148, Spirit Bay, New Zealand, larvae.

USNM 343321, Market South of town of Valparaiso, Chile, Pacific, Recent skeleton.

USNM 343322, Market South of town of Valparaiso, Chile, Pacific, Recent skeleton.

USNM 2875229, New South Wales, Australia, Recent skeleton.

THYRSITOIDES

T. marleyi

BMNH 1986.9.8.147, off Indonesia, spirit specimen (x-rayed).

TRACHURUS

T. mediterraneus

BMNH 1982.5.10.169-178, St. George's Bay, R. of Lebanon, spirit specimens, one of which cleared and stained.

T. trachurus

BMNH "135a", England, Recent skeleton.

BMNH 1861.11.20.28, Gibraltar, spirit specimen (x-rayed).

BMNH 1972.12.6.97, Ulsac, Isles of Scilly, spirit specimen.

BMNH uncat., Port Jackson, Australia, Recent skull.

†TRICHIURIDAE INDET.

BMNH 41318 (labelled as *Eutrichiurides*?), Sheppey, England, Ypresian (London Clay).

TRICHIURUS

T. lepturus

BMNH 1862.11.23.6-7, Bahia, spirit specimens (one of which x-rayed).

BMNH 1939.5.3.22-24, Haifa, Israel, spirit specimens, one of which cleared and stained.

BMNH 1889.2.1.3173 (labelled as *Trichiurus haumela*), Madras, India, Recent skeleton

USNM 111241 (labelled "*Trichiurus*"), New Caledonia, Pacific, Dried specimen.

USNM 111242 (labelled "*Trichiurus*"), New Caledonia, Pacific, Recent skeleton.

USNM 111246 (labelled "*Trichiurus*"), New Caledonia, Pacific, Recent skeleton.

USNM 270762 (formerly USNM Bone 25845 and in box with USNM 270763), Beaufort, North Carolina, U.S.A., Atlantic, Recent skull.

USNM 270763 (formerly USNM Bone 25846 and in box with USNM 270762), from Army Med. Mus., Recent skeleton.

USNM 270771 (formerly USNM Bone 27405), Cedar Key, Florida, U.S.A., Gulf of Mexico, dried skeleton and head.

USNM 273478, (labelled Trichiuridae), Playa de Pina Fish Market, Recife, Brazil, Recent skeleton.

†*T.* aff. *lepturus*

USNM 291178, South side of Pamlico River, near Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., Miocene (Fish Stratigraphic Column, Pungo River Formation).

†*T.* sp.

BMNH P24270-9 (stored as *Trichiurus oshosunensis*), Oshosun, South Nigeria, Lutetian.

†UNKNOWN

BMNH P12955 (labelled *Xiphiorhynchus*), Sheppey, England, Ypresian (London Clay).

BMNH P14641-2, no data.

BMNH P15391-4, no data.

BMNH P15398-9, no data.

BMNH 25739 (identical to BMNH25819, see below), Bracklesham, England, Ypresian-Lutetian (Bracklesham Beds).

BMNH 25740 (identical to BMNH25819, see below)., Bracklesham, England, Ypresian-Lutetian (Bracklesham Beds).

BMNH 25819, **Holotype** of *Sphyraenodus tenuis*, Bracklesham, England, Ypresian-Lutetian (Bracklesham Beds).

BMNH 25819a (labelled as "scombroid"), Bracklesham, England, Ypresian-Lutetian (Bracklesham Beds).

BMNH 30530 (labelled as *Xiphiorhynchus cf. priscus*), Sheppey, England, Ypresian (London Clay).

BMNH 35270 (labelled as *Xiphiorhynchus cf. priscus*), no data.

BMNH P26709 (*Planesox vorax*), Sheppey, England, Ypresian (London Clay).

BMNH P11853 α (**Holotype**) and β (**Paratype**) of *Scombramphodon woodwardi*, near Ameki, Southern Nigeria, Lutetian.

VALAMUGIL

V. buchananii

BMNH 1974.5.25.3590-3602, Trobiands Bay, cleared and stained specimens.

BMNH 1981.4.9.315, Subaki R., Lower Athi, Kenya, spirit specimen.

V. engeli

BMNH 1905.12.1.7-10, Tahiti, cleared and stained specimens.

BMNH 1955.1.18.103-113, Javad Ghasemzadeh, 53-68 mm, cleared and stained specimens.

BMNH 1955.1.18.112-113 (labelled as *Liza engeli*), R. Subaki, Kenya, cleared and stained specimens.

†*WETHERELLUS*

W. cristatus

BMNH 269891, **Holotype** of *Wetherellus brevior*, Sheppey, England, Ypresian (London Clay).

BMNH 28498, **Holotype** of *Wetherellus cristatus*, Sheppey, England, Ypresian (London Clay).

BMNH P26719 (old P1698), **Paratype** of *Wetherellus cristatus*, Sheppey, England, Ypresian (London Clay).

BMNH P45045 (old P1758a), **Paratype** of *Wetherellus cristatus*, Sheppey, England, Ypresian (London Clay).

BMNH P45047 (old 30893), **Holotype** of *Wetherellus longior*, Sheppey, England, Ypresian (London Clay).

BMNH P45048 (old 38093a), **Paratype** of *Wetherellus cristatus*, Sheppey, England, Ypresian (London Clay).

†*WOODWARDELLA*

W. patellifrons

BMNH P26903, **Holotype**, Sheppey, England, Ypresian (London Clay).

XIPHIAS

X. gladius

BMNH 1846.9.11.91, no data, larva.

BMNH 1867.10.8.61, St. Helena, juvenile spirit specimen.

BMNH 1895.6.30.17, New South Wales, Australia, rostrum of Recent specimen.

BMNH uncat., Madiera, Portugal, juvenile spirit specimen.

†USNM 47639 (see also Fierstine, 2000, Fig. 79 J-K), South side of Pamlico River, Aurora, Beaufort Co., Lee Creek Mine, North Carolina, U.S.A., rostrum fragment, Early Pliocene: Zanclean (Yorktown Formation).

USNM 270770 (formerly Mam. Cat. 11850), Woods Hole, Massachusetts, U.S.A, Atlantic, dried gills.

USNM 285038, no data, Recent skeleton.

USNM 316703, 32°30'N, 76°54'W, Atlantic, Recent skeleton.

USNM 316704, East Pacific, Recent skeleton.

USNM 316705, Atlantic, 33°34'N, 76°36'W, Recent skeleton.

USNM 316706, East Pacific, Recent skeleton.

†***XIPHIORHYNCHUS***

X. eocaenicus

BMNH P25744 (**Holotype** of *Histiophorus eocaenicus*), Bracklesham, England, Ypresian-Lutetian (Bracklesham Beds).

X. priscus

BMNH 3888 (labelled as *Xiphiorhynchus sp.*), Sheppey, England, Ypresian (London Clay).

BMNH 28711, Sheppey, England, Ypresian (London Clay).

BMNH 32387, Sheppey, England, Ypresian (London Clay).

BMNH P12204 (labelled as *Histiophorus eocaenicus*), East shore, Selsey, England, Bartonian (Selsey Sands, Bracklesham Beds).

BMNH P13506, Sheppey, England, Ypresian (London Clay).

BMNH P19492 (labelled as *Xiphiorhynchus sp.*), Beltinge, Herne Bay, Kent, England, Ypresian (London Clay).

BMNH P26990, Sheppey, England Ypresian (London Clay).

BMNH 36133a, Sheppey, England, Ypresian (London Clay).

X. ?antiquus

USNM 353509, 6.4 km by road W of Post Office at a few hundreds of meters N of State Route 41, immediately W of Tuckahoe Church, Jones Co, North Carolina, U.S.A., Eocene (Claibornain Castle Hayne Formation).

APPENDIX 2: ABBREVIATIONS OF OSTEOLOGICAL TERMS

A	Angular	**F**	Fang
1A	First anal fin (billfishes)	**f**	Finlet
2A	Second anal fin (billfishes)	**fpf**	Fronto-parietal fenestrum
AC	Actinost	**FR**	Frontal
AF	Anal fin	**GH**	Glossohyal
ap	Ascending process of premaxilla	**HG**	Hyoidean groove
		HH	Hypohyal
ASPH	Alisphenoid	**HP**	Hypural plate
BOC	Basioccipital	**hpu**	Haemal spine of preural centrum
BR	Branchiostegal ray		
BSPH	Basisphenoid	**HA**	Haemal arch
C	Centrum	**HB**	Hypobranchial
CB	Ceratobranchial	**hs**	Haemal spine
CC	Cranial crest	**HY**	Hyomandibular
cc	Central canal	**HYP**	Hypural
CD	Continuous dorsal fin	**hys**	Hyomandibular spine
CF	Caudal fin	**IC**	Intercalar
CH	Ceratohyal	**is**	Inner side of cleithrum
CK	Caudal keel	**IO**	Infraorbital
CL	Cleithrum	**IOP**	Interoperculum
COR	Coracoid	**KLP**	Keel-like process
CS	Cycloid scale	**LA**	Lachrymal
D	Dentary	**LETH**	Lateral ethmoid
dHH	Dorsal hypohyal	**LK**	Lateral keel
dhp	Dorsal hypural plate	**LLS**	Lateral line scale
dp	Dorsal process	**META**	Metapterygoid
DR	Distal radial	**MK**	Midlateral keel
DPCL	Dorsal postcleithrum	**mp**	Median process
1D	First dorsal fin	**MX**	Maxilla
2D	Second dorsal fin	**N**	Caudal notch (hypural plate)
E	Epural		
EB	Epibranchial	**n**	Remnant of Caudal notch
ECTO	Ectopterygoid	**nc**	Nutrient canal
EH	Epihyal	**NA**	Neural Arch
ENTO	Entopterygoid	**NAS**	Nasal
EPI	Epiotic	**ns**	Neural spine
ETH	Ethmoid	**OP**	Operculum
EXOC	Exoccipital	**os**	Outer side of cleithrum

P	Palatine
PP	Pelvic plate
PAR	Parietal
PB	Pharyngobranchial
PCL	Postcleithrum
PD	Predorsal
PELF	Pelvic fin
pelfr	Pelvic fin ray
pelfs	Pelvic fin spine
PF	Pectoral fin
pf	Posttemporal fossa
PHP	Parhypural
phps	Parhypurapophysis
plp	articulation protuberance for lower limb of PTM
PMR	Proximal-middle radial
PMX	Premaxilla
POP	Preoperculum
POSTZ	Postzygapophysis
PP	Pelvic plate
PPD	Pseudo-predorsal
PRED	Predentary
PREZ	Prezygapophysis
PROO	Prootic
PRPS	Parapophysis
ps	Procurrent spur
psf	Postero-superior fossa
PSP	Parasphenoid
PT	Pterotic
PTM	Posttemporal
PTR	Pterygiophore
ptp	Palatinal tooth plate
PU	Preural (vertebra)
PV	Pelvic fin
pw	Pineal window
Q	Quadrate
R	Rib
RA	Retroarticular
SC	Sclerotic
SCL	Supracleithrum
SO	Supraoccipital
SOC	Supraoccipital crest
SOP	Suboperculum
sp	Symphysial process of dentary
SPH	Sphenotic
SUPM	Supramaxilla
SQ	Squamosum
ST	Serial tooth
STM	Supratemporal
SY	Symplectic
stg	Supratemporal groove
tg	Temporal groove
TS	Rigid tubercule/tubular scale
ts	Tooth socket
U	Ural centrum
UH	Urohyal
UN	Uroneural
US	Urostyle
V	Vomer
vHH	Ventral hypohyal
vhp	Ventral hypural plate
VPCL	Ventral Postcleithrum
vp	Ventral process
vtp	Vomerine tooth plate

APPENDIX 3: LIST OF CHARACTERS

1. Relative size of lachrymal. 0: Small, shorter than diameter of orbit 1: large, at least as long as diameter of orbit (§ 5.2.1.1, section Infraorbitals).

2. Supratemporal groove. 0: Short. 1: Long:, extending over the whole length of frontal, laterally bordered by frontoparietal crest (§ 5.2.1.1, section Supratemporal groove).

3. Postero-superior fossa: 0: Clearly posterior to middle of orbit, 1: Near middle of orbit. 2: Almost at anterior edge of orbit (§ 5.2.1.1, section Postero-superior fossa).

4. Frontoparietal fenestra: 0: Absent. 1: Present (§ 5.2.1.1, section Frontoparietal fenestra).

5. Pineal window: 0: Absent, 1: Present (§ 5.2.1.1, section Pineal window).

6. Cranial crest. 0: Absent. 1: Low and short cranial crest, less deep than underlying cranium and not extending to anterior tip of frontals 2: As 1, but extending to anterior tip of frontals. 3: Crest deeper than underlying cranium and extended far anteriorly (§ 5.2.1.1, section Cranial crest).

7. Anterior margin of ethmoid. 0: Protruding. 1: Emarginated (§ 5.2.1.1, section Ethmoid).

8. Pterotic. 0: A short wing. 1: Furnished with a long "pterotic spine" (§ 5.2.1.1, section Pterotic).

9. Apex of epiotic. 0: Normally pointed, or in some cases, bifurcated, 1: Apex fimbriated, like a brush (§ 5.2.1.1, section Epiotic).

10. Caudal projection of Intercalar: 0: None, 1: Short, barely projecting, 2: Long, clearly projecting (§ 5.2.1.1, section Intercalar).

11. Supramaxilla: 0: Present (plesiomorphous), 1: Absent (§ 5.2.1.2, section Supramaxilla).

12. Premaxilla: 0: Protrusible: not tightly bound together, loosely connected, 1: Non-protrusible: tightly bound complex, maxilla snugly fits onto premaxilla (§ 5.2.1.2, section Premaxilla).

13. Teeth on vomer: 0: Present, 1: Absent (§ 5.2.1.1, section Vomer).

14. Anterior margin of vomer 0: Emarginated or blunt, at most with short, inconspicuous protrusion. 1: Anterior margin with strongly protruding, spatula-like projection (§ 5.2.1.1, section Vomer).

15. Teeth on palatine: 0 Present, 1: Absent (§ 5.2.1.2, section Palatine).

16. Larval beak: 0: Short-snouted, 1: Elongate and horizontal (§ 5.4.1).

17. Cartilagenous ridges on tongue: 0: Absent, 1: Present (§ 5.3.1.2).

18. Rostrum: 0: Absent, 1: Oval, depth more than 1/2 of width, denticles present, never with central chambers, 2: Flattened, depth less than 1/2 of width, denticles absent, central chambers present (§ 5.2.1.3).

19. Relative jaw (incl. rostrum) lengths: 0: Upper jaw up to twice as long as lower jaw from articulation point on, 1: More than twice as long, 2: Lower jaw longer (§ 5.2.12 section Dentary; § 5.2.1.3) .

20. Rows of serial teeth: 0: Present, in a single row, 1: Present, in incomplete double row. 2: Present, in complete double row. 3: Multiple rows. 4: Absent (§ 5.2.1.2, section Dentition).

21. Fangs: 0: Absent, 1: Present (§ 5.2.1.2, section Dentition).

22. Shape of serial teeth and interspacing. 0: Conical or somewhat flattened, but always sharp-pointed. 1: straight, laterally compressed and unserrated, always tightly packed. 2: As in 1, but teeth with serrated cutting edges.

23. Curvature of serial teeth. 0: Straight. 1: Retrorse.

24. Nostrils: 0: Double, 1: Single (§ 5.3.1.1).

25. Prenasal: 0: Absent, 1: Present (see ill. in Suda) (§ 5.2.1.3, Prenasal).

26. Ceratohyal: 0: Ventrally smooth and straight, apart from sockets for branchiostegal rays, 1: Furnished with small projections (§ 5.2.1.2, section Hyoid complex).

27. Ceratohyal window: 0: Absent, 1: Present (§ 5.2.1.2, section Hyoid complex).

28. Last branchiostegal ray: 0: At most slightly flattened, 1: Forming wide plate (§ 5.2.1.2, section Hyoid complex).

29. Unique 2nd epibranchial-3rd pharyngobranchial articulation. 0: Absent, 1: Present (§ 5.2.1.2, section Pharyngobranchial).

30. Fourth Pharyngobranchial cartilage. 0: Present, 1: Absent (§ 5.2.1.2, section Pharyngobranchial).

31. Triangular stay from 4th pharyngeal tooth plate to 3rd pharyngobranchial. 0: Absent, 1: Present (§ 5.2.1.2, section Pharyngobranchial).

32. Gill filaments modified: with denticles and bony or cartilagenous interconnections 0: Not modified like that, 1: Modified like that (§ 5.3.1.3).

33. Gill rakers: 0: Arches fully occupied by splint-like rakers, 1: Number of splint-like rakers greatly reduced, 2: Nil (§ 5.2.1.2, section Gill rakers).

34. Branchiostegal regions: 0: Distally separated, 1: Left and right regions united (§ 5.3.1.4).

35. Operculum: 0: Not indented posterodorsally, 1: indented (§ 5.2.1.2, section Operculum).

36. Except Preoperculum, one to all of the opercular elements fringed: 0: Not like this, 1: Like this (§ 5.2.1.2, section Opercular series).

37. Ventral margin of suboperculum: 0: Convex, 1: Concave (§ 5.2.1.2, section Suboperculum).

38. Number of vertebrae 0: 23-26, 1: 28-64, 2: 76-174 (§ 5.2.2.1).

39. General shape of vertebrae. 0: Narrow part considerably thicker than one third of the thickest end, 1: Almost a third of the thickest end (§ 5.2.2.2).

40. Mid-lateral dent in vertebrae. 0: Absent. 1: With a large, fully developed mid-lateral dent.

41. Neural and haemal spines. 0: Spiniform (somewhat flattened in *Xiphias*). 1: Spine bifurcated: two-pronged spine, two prongs of unequal lenght 2: Spine bifurcated with anterior branch flattened into plate-like structure (due fossilisation sometimes resembling state 1). 3: one massive plate (§ 5.2.2.3).

42. First haemal spine articulates with: 0: Anal fin pterygiophore 1, 1: anal fin pterygiophore >1 (§ 5.2.4.4).

43. Preural vertebrae: 0: Not remarkably shortenend. 1: Preural 2-preural 3/4, compared to preceding vertebrae abruptly shortened, haemal and neural spines dorso-ventrally flattened and partially cover the subsequent vertebra (§ 5.2.3.7).

44. Neural and haemal spines of preural vertebrae. 0: Spiniform. 1: Laterally flattened and apically widened into fan-shape (§ 5.2.3.7).

45. Thin-walled lateral bullae on vertebrae 5-12. 0: Absent, 1: Present (§ 5.2.2.2).

46. Bony lateral caudal keel: 0: Absent, 1: Present, weakly developed, 2: Present, fully developed (§ 5.2.2.6).

47. Mid-lateral fleshy caudal keel. 0: Absent, 1: With weakly developed fleshy keel, 2: With fleshy keel well developed (§ 5.3.3.1).

48. 2 Fleshy lateral caudal keels (on each side): 0: Absent, 1: Present (§ 5.3.3.2).

49. Caudal complex: 0: Present. 1: Absent.

50. Median caudal fin rays: 0: Normal, 1: Enlarged and widely spaced (§ 5.2.4.9).

51. Hypurostegy. 0: no, 1: yes (§ 5.2.4.9).

52. Number of epurals. 0: three, 1: two, 2: one (§ 5.2.3.6).

53. Hypural plate (hypurals 1-4). 0: all elements autogenous (plesiomorphous). 0: Clearly split in a dorsal and a ventral part with hypurals 1 and 2 separate. 2: Clearly split in dorsal and ventral part with hypurals 1 and 2 fused. 3: Elements fully fused and a distal notch. 4: as 3, but then with only a small, hard to spot vestige as a relic of the notch. 5: As in 3, no notch. (§ 5.2.3.1-2).

54. Fifth Hypural. 0: Unfused to hypural plate, 1: Partially fused, 2: Completely fused, 3: Not appearing in ontogeny (§ 5.2.3.2).

55. Parhypural. 0: Not fused to hypural plate, 1: Fused (§ 5.2.3.5).

56. Procurrent spur: 0: Present, 1: Absent (§ 5.2.4.9).

57. Posttemporal: 0: 2 anterior processes, 1: 3 processes (§ 5.2.4.5, section Posttemporal).

58. Number of pelvic fin rays. 0: I+5, 1: 5, 2: I+1-4, 3: I (§ 5.2.4.8).

59. Pelvic fins: 0: Longer than interpelvic process, 1: Shorter than interpelvic process.(§ 5.2.4.8).

60. Predorsal bones: 0: Present, 1:Absent, 2: Pseudo-predorsals (§ 5.2.4.2).

61. First dorsal pterygiophore or pseudo-predorsal in : 0: 3rd Interhaemal space, 1: 1st or 2nd Interneural space, 2: 4th Interneural space or beyond (§ 5.2.4.3 section, First dorsal).

62. Modified configuration of dorsal pterygiophore-elements (char. 21 & 22 in Johnson, 1986). 0: Not: proximal-middle and distal radials overlap slightly, distal radial only loosely connected to proximal-middle radial (plesiomorphous), 1: Modified configuration: proximal-middle and distal radial overlap extensively, distal radial locks snugly on process of proximal-middle radial (§ 5.2.4.3 section, First dorsal).

63. Association of soft dorsal pterygiophores with neural spines: 0: Not fully. 1: Fully (§ 5.2.4.3, section Second dorsal).

64. Dorsal fins: 0: Connected, almost connected or no distinction clearly visible, 1: Not connected, a wide space between the 2 dorsal fins (§ 5.2.4.3).

65. First dorsal: 0: Spinous, 1: Soft (§ 5.2.4.3 section, First dorsal).

66. First dorsal fin: 0: Anterior lobe less than twice as high as remainder of fin, fin height more or less gradually declining posteriorly, or no real anterior lobe. 1 Anterior lobe twice or more as high as remainder of rest of fin, 2: Anterior lobe not

or not by far the highest point of this fin and maximum height of fin higher than body depth.

67. Number of 1st dorsal fin rays. 0: 2-23, 1: 30-51, 2: 58-71, 3: 97-107 (§ 5.2.4.3 section, First dorsal).

68. First dorsal: 0: Not as deep as maximum depth of head (plesiomorphous), 1: As deep or deeper (§ 5.2.4.3 section, First dorsal).

69. Number of 2nd dorsal fin rays. 0: No distinction between 1st and 2nd dorsal 1: 98-142, 2: 29-85, 3: 7-23 (§ 5.2.4.3, section Second dorsal).

70. Second dorsal fin spine. 0: Absent (plesiomorphous), 1 Present, with 1 or 2 (§ 5.2.4.3, section Second dorsal).

71. Configuration of soft dorsal and anal fin pterygiophores. 0: Two autogenous radials: proximal-middle and radial. Absent (plesiomorphous), 1: Three autogenous radials: proximal, middle and distal; and distal radial embraced by soft fin ray (§ 5.2.4.3 section, Second dorsal).

72. Number of anal fin rays: 0: 7-44 (plesiomorphous), 1: 45-68, 2: 74-108 (§ 5.2.4.4).

73. Anal fin spines. 0: Present, 1, 2 or 3 (plesiomorphous), 1: Absent (§ 5.2.4.4).

74. Number of finlets (anal or dorsal). 0: 0 (plesiomorphous), 1: Distinction of 2 sections of anal fin, but still interconnected, 2: As a '2nd dorsal/anal', with 3-9 rays, 3: 2-3, 4: 4-10 (§ 5.2.4.3, section Finlets).

75. Pelvic plate. 0: Anterodorsal plate simple, maybe consisting of different wings, but not really differentiated. 1: Anterodorsal plate consisting of 3 wings: external, internal and vertical, clearly differentiated, pointing in different directions, giving the structure a more complex outlook.(§ 5.2.4.7). 2: pelvic plate missing.

76. Location of dark muscles. 0: At the outer margin of the myotome (plesiomorphous). 1: In the middle of the myotome, 2: Forming a band between the centrums and the outer margin of the myotome (§ 4.1).

77. Heater system: 0: Absent (plesiomorphous). 1: Present, derived from lateral rectus muscle (*Gasterochisma*) 2: Derived from superior rectus muscle 3:

Systemic endothermy with neothunnoid-heater exchange system (§ 4.1). 4: Systemic endothermy with thunnoid heater-exchange system.

78. Swimbladder in adults: 0: Present, consisting of one sole chamber (plesiomorphous) 1: present, consisting of several small chambers, 2: Absent or rudimentary (§ 5.3.4).

79. Scales: 0: Large scales all over (plesiomorphous), 1: Moderate-sized scales all over, 2: Small scales all over, 3: Scaleless or almost, with anterior corselet, 4: Ventral corselet, 5: Scaleless or almost, no anterior corselet (§ 5.3.2.1).

80. Larvae: 0: "Normal", 1: With a set of unique synapomorphies: deep, serrated dorsal spine, short but precocious pelvics (*sensu* Collette *et al.*, 1984), 2: as in 1, but with a deeper first dorsal fin, larger pelvics and a preopercular spine (§ 5.4).

APPENDIX 4: SCOMBROID DATA MATRIX

The following fold-out contains the data matrix in, its original format, which was the input source for the cladistic analyses in PAUP*.

Explanation of symbols

* in character entry	information of entry drawn from literature reference(s)
* in taxon entry	all data of taxon drawn from literature reference(s)
†	taxon represented only by fossils
(character states)	multistate character treated as polymorphism
{character states}	multistate character treated as uncertainty
M	feature absent from studied specimen, character cannot be scored
?	character state of feature unclear from studied specimens, character cannot be scored
N	Inapplicable